

GROWTH OF FISHES IN THE MISSOURI RIVER AND LOWER YELLOWSTONE
RIVER, AND FACTORS INFLUENCING RECRUITMENT OF FRESHWATER
DRUM IN THE LOWER CHANNELIZED MISSOURI RIVER

by

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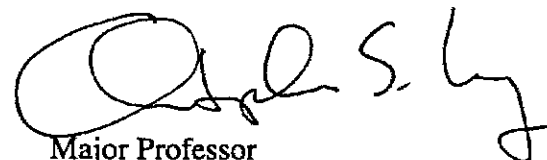
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Preface

Population Structure and Habitat Use of Benthic Fishes along the Missouri and Lower Yellowstone Rivers

This research is reported in 12 volumes. Final Report volumes are listed below and are available from the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15th Street, Omaha, NE 68102 (rebecca.j.latka@usace.army.mil, 4021221-4602) for copies. Volumes are currently available unless indicated otherwise (anticipated date of publication).

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- Young. 2001 Intraspecific variation among emerald shiners (*Notropis antherinoides*) of the Missouri River. Ph.D. Dissertation, South Dakota State University, Brookings, South Dakota. Volume 11 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.
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- Berry, C. and D. Galat. 2001. Synopsis of the population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone rivers. Agriculture Experiment Station Bulletin 7xx, Available from: Bulletin Room, LMH112, South Dakota State University, Brookings, South Dakota 57007. (available August 2001)

ABSTRACT

The first goal of this study was to discern patterns of growth and other life history characteristics of five fish species (emerald shiner *Notropis atherinoides*, sicklefin chub *Macrhybopsis meeki*, freshwater drum *Aplodinotus grunniens*, river carpsucker *Carpiodes carpio*, sauger *Stizostedion canadense*) sampled from 18 Missouri River segments varying from 38° 47' North to 48° 03' North. Populations in southern latitudes were shorter-lived, and had higher life-span growth rates than northern latitude populations. Growth increments (mm) of all species during the first and second growing seasons varied among latitudes, but growth rates (mm/degree-day, mm/day) increased from south to north for all species except sauger for which growth rates declined from south to north. Species exhibited differential growth responses to water velocity. Within river segments, growth increments were related to median discharge during the growing season in 30% of the species by river segment analyses; however, growth responses to discharge varied among species and river segments. Results suggest growth and life-history patterns of fishes in the Missouri River are strongly influenced by the thermal regime which varies directly with latitude. At reduced spatial scales (i.e., within segments), interannual variations in river discharge mediate differential fish growth.

The second goal of this study was to examine factors influencing recruitment of freshwater drum in the channelized Missouri River. Larval and age-0 freshwater drum were sampled during 1997 and 1998 at four study sites located 514, 581, 699, and 788 km downstream from Lewis and Clark Lake - an upstream spawning area and source of larval freshwater drum. Larval density declined from upstream to downstream in 1998, providing evidence that upstream areas were the primary spawning locations and sources

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Chapter 1

Differential growth responses by fishes to latitude and discharge in the Missouri River basin

Introduction

Numerous fish species are widely distributed throughout North America (Lee et al. 1980), and maintain populations in a diversity of streams and rivers (Matthews 1987). Thus, individual species inhabiting lotic environments across a broad geographic range are subject to varying environmental factors. Persistence of populations throughout a broad geographical range suggests species have broad physiological tolerances to environmental conditions (Matthews 1987) or exhibit environmental adaptations derived through phenotypic plasticity (Stearns 1989).

Natural environmental gradients of productivity, temperature, and water velocity occur in lotic ecosystems, and may strongly influence growth in fishes. First, across broad spatial scales, rivers vary substantially in productivity and discharge from upstream to downstream reaches (Vannote et al. 1980). As a consequence, variations in fish growth along a river may reflect natural variations in aquatic productivity (Mann et al. 1984). In association with longitudinal variation in river productivity, evidence from floodplain rivers strongly suggests that interannual variations in fish growth are closely linked to the magnitude and duration of high discharge, where fish growth and aquatic production increase with increasing discharge (i.e., the flood pulse; Welcomme 1979; Bayley 1988; Junk et al. 1989; Bayley 1991; Welcomme 1995; Gutreuter et al. 1999; but

see Thorp et al. 1998). However, in modified river systems where the floodplain has been reduced or isolated from the river, positive correlations between fish growth and river discharge may not occur (Rutherford et al. 1995). Similarly, the flood pulse mechanism may not be equally applicable to all reaches along a river gradient because flood duration and retention times vary from upstream to downstream (Bayley 1991).

Natural variations in water temperature and duration of the growing season that occur across a broad latitudinal gradient impose on fishes differential constraints that influence growth and other life history parameters. Body size of fishes generally increase from south to north (e.g., Bergmann's rule, Lindsey 1966; Winemiller 1991; Holcik and Jedlicka 1994; Taylor and Gotelli 1994), but this pattern is not always exhibited for all age classes (Roni and Quinn 1995; Lobon-Cervia et al. 1996). Similarly, studies have shown that fish longevity increases from southern to northern latitudes (Colby and Nepszy 1981; Beverton 1987); whereas, mortality rates decline from south to north (Colby and Nepszy 1981; Beverton 1987; Beamesderfer and North 1995). Growth rates throughout the life span also increase from north to south (Beverton 1987; Lobon-Cervia et al. 1996) due to the direct influence of water temperature on growth rate (Beverton 1987). Lastly, strong evidence suggests that fishes in northern latitudes exhibit higher growth rates than fishes in southern latitudes (e.g., countergradient growth variation, Conover 1990; Conover and Present 1990; Lobon-Cervia et al. 1996; Arendt 1997; Conover et al. 1997, Power and McKinley 1997). Thus, latitude and its thermal correlates impose natural life history trade-offs (e.g., Stearns and Crandall 1984) in

longevity and mortality that mediate differential growth patterns across broad latitudinal gradients in rivers.

Water velocity represents a third environmental gradient that influences growth of fishes in large rivers. Different water velocities exhibit varying force and drag on aquatic organisms (Gordon et al. 1992; Vogel 1994; Sagnes et al. 1997), and in general, the morphology of aquatic organisms is structured to minimize drag with respect to their life history characteristics (Webb 1984; Sagnes et al. 1997). Increases in velocity from upstream to downstream (Gordon et al. 1992; Allan 1995) may impose greater energetic demands on fishes in downstream reaches and reduce growth rates if velocity use by a species varies along a river.

Natural, large-scale patterns in growth and other life history parameters along a river may be altered if anthropogenic modifications acting at smaller regional scales exhibit greater regulatory control on fish populations. For example, Przybylski (1996) documented differences in length-weight relationships and lifespan growth patterns among natural and modified sections of the same river. Torralva et al. (1997) found growth, maturity schedules, and condition of fish differed between a high-velocity channelized river section and a natural river section. Although the Missouri River in its natural state was likely characterized by natural gradients of discharge, productivity, water temperature, and velocity from upstream to downstream as predicted for natural rivers (Vannote et al. 1980; Junk et al. 1989), the present-day Missouri River has been extensively modified by dam construction, flow regulation, and channelization throughout much of its length which have altered instream habitat, productivity, and

thermal conditions (Hesse et al. 1989). The effects of these anthropogenic modifications on fish growth in the Missouri River are not specifically known.

This study was designed to examine growth of five widely distributed fish species (emerald shiner *Notropis atherinoides*, sicklefin chub *Macrhybopsis meeki*, freshwater drum *Aplodinotus grunniens*, river carpsucker *Carpiodes carpio*, sauger *Stizostedion canadense*) throughout the Missouri River basin which included more than 2,300 km of the Missouri River and lower Yellowstone River. The first objective was to examine variations in life history parameters (i.e., longevity, length at age, von Bertalanffy growth trajectories) among river segments, and discern relations between these parameters and latitude. The second objective was to compare growth increments and growth rates of fishes during the first and second growing seasons among latitudes differentially impacted by anthropogenic modifications. The third objective was to examine relations between growth and latitude and water velocity used by fishes. I focused on growth during the first and second growing seasons for two reasons. First, factors influencing growth during these early life stages can strongly influence survival to adulthood. Second, I was primarily interested in comparing rates of somatic growth among river segments. Restricting the analysis to the first two growing seasons prevented differential partitioning of energy into somatic and gonadal growth from confounding the analyses. The fourth objective was to examine relations between growth during the first and second growing seasons and segment-level discharge.

Study Area

The Missouri River is the longest river (3,768 km) in the United States, and drains 135 million-ha of the continental United States, and 2.5 million ha of Canada (Hesse et al. 1989). It originates at the confluence of the Gallatin, Madison, and Jefferson rivers in Montana and flows in an east-southeast direction to its confluence with the Mississippi River near St. Louis, Missouri (Figure 1). The river changes from a cold- to warmwater fishery near Loma, Montana (White and Bergstedt 1995). Mean annual discharge increases 10-fold between segment 1 (228 m³/s) and segment 27 (2,630 m³/s; Galat and Lipkin 1999).

Physical habitat conditions vary substantially along the Missouri River. Between 1937 and 1963, six multipurpose (e.g., flow regulation, hydropower generation, flood control) mainstem dams were completed in the upper two-thirds of the Missouri River (Figure 1). All dams except Gavins Point dam, the most downstream dam, have hypolimnetic intake structures which result in lower water temperatures in reaches directly downstream. Reduced water temperature is most prevalent in river reaches downstream from Fort Peck, Garrison, and Oahe dams due to summer stratification in the reservoirs (Hesse et al. 1989). Water drawn through Gavins Point Dam is extracted from near the reservoir surface to the bottom (Walburg 1971); therefore, water temperature downstream from Gavins Point Dam is not significantly lowered. Turbidity generally increases from upstream to downstream with the exception of river reaches downstream from dams where turbidity is reduced (Dieterman et al. 1996; Young et al. 1997). Channel degradation (downcutting) occurs in reaches downstream from dams due to

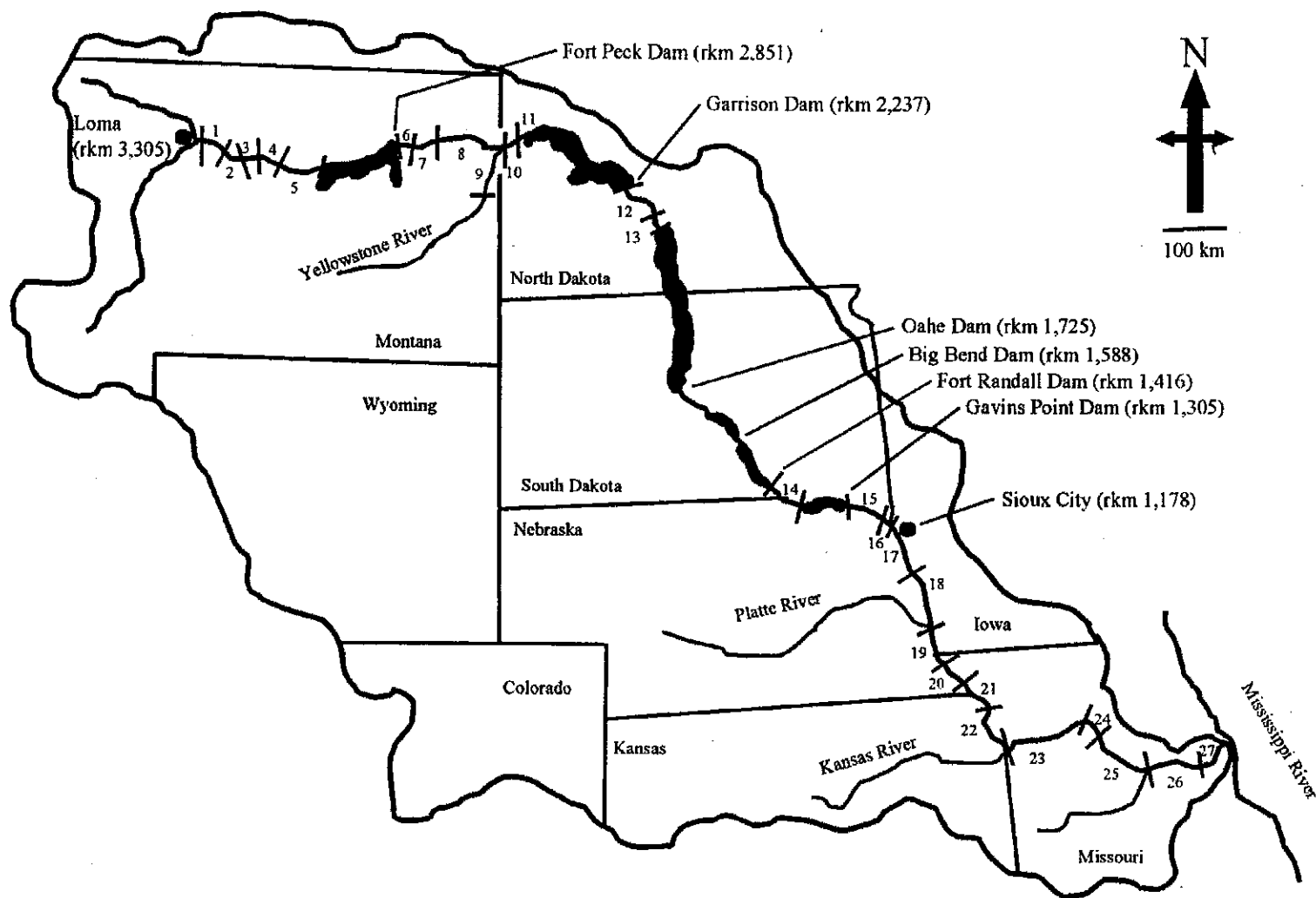


Figure 1.-Study area and segments of the Missouri River and Yellowstone River. River kilometer (rkm) is the distance upstream from the confluence with the Mississippi River. Adapted from Hesse et al. (1989).

deposition of sediments in the reservoirs (Hesse et al. 1989; Latka et al. 1993). As a consequence, inundation of backwaters and other off-channel habitats may occur only during extreme discharge releases through the dams. The lower one-third of the Missouri River from Sioux City, Iowa to the mouth is channelized. Wing dikes along inside bends concentrate the majority of the river flow into a navigable river channel (Slizeski et al. 1982), and have eliminated most of the secondary channels and other off-channel and floodplain habitats (e.g., backwaters) characteristic of the natural Missouri River (Funk and Robinson 1974). Shorelines on outside bends of the channelized Missouri River are lined with riprap, further concentrating flows into the main channel and minimizing lateral migration of the river channel. Discharge releases through Gavins Point Dam primarily influence flow levels in the upper reaches of the channelized river, but these flows are augmented in the lower channelized river with inputs from large tributaries. Discharge releases from Gavins Point Dam are increased during April-November to accommodate navigation needs in the channelized river, then decreased during the winter months.

The Yellowstone River originates in Wyoming and drains 182,336 km² (White and Bramblett 1993). It joins the Missouri River at river kilometer 2,547 (rkm; distance upstream from the Mississippi River), about 300 rkm downstream from Fort Peck dam (Figure 1). Mean annual discharge near the river mouth is 362 m³/s (White and Bramblett 1993). There are no dams on the mainstem Yellowstone River; however, a diversion dam is located at rkm 114. Instream habitat in the Yellowstone River is similar to natural conditions (White and Bramblett 1993).

Methods

The Missouri River and lower 114 km of the Yellowstone River were partitioned into 27 river segments, labeled consecutively from 1 (most upstream) to 27 (most downstream) based on changes in river morphology, discharge, tributary inputs, and other hydrophysical characteristics along the river channel (Figure 1). For example, segment 8 ends above the Yellowstone River and segment 10 starts below the confluence of the Yellowstone River. Similarly, reaches below dams were designated as river segments because hydrological characteristics downstream from dams differ (e.g., water temperature, turbidity, etc.) from the nearest segment upstream from the reservoir. Although 27 segments were identified, not all segments were used in the study due to logistical constraints. Median latitude of the segments studied varied from 38° 47' North (segment 27) to 48° 03' North (segment 8).

Fish sampling.-Emerald shiners, sicklefin chubs, freshwater drum, river carpsucker, and sauger were sampled in river segments between mid-July and October during 1996, 1997, and 1998. Detailed discussions of sampling gears and standard sampling procedures are outlined in Sappington et al. (1996, 1998). Seines, boat electrofishing, drifting trammel nets, stationary gill nets, and benthic trawls were used to sample fish in habitats conducive to each gear. Habitats sampled included sand bars, natural and wing-dike pools, main channel (i.e., shoreline, thalweg), main channel border (i.e., located between the thalweg and inside bend shoreline), wing dikes (channelized river only), tributary confluences, secondary channels (e.g., flowing and non-flowing channels off from the main channel), and any unique habitats that occurred in river

segments. The variety of gears used facilitated sampling of all life stages in all habitats characteristic of each segment. A total of 18 river segments were sampled during 1996 (segments 3, 5, 6, 7, 8, 9, 10, 12, 14, 15, 17, 18, 19, 21, 22, 23, 25, 27); whereas, 15 river segments excluding segments 6, 18, and 21 were sampled during 1997 and 1998.

Age and Growth

Treatment of individuals for age and growth estimates varied among species. Emerald shiners and sicklefin chubs collected in the field were preserved in 10% buffered formalin for later processing. Total length (TL; mm) of freshwater drum, river carpsuckers, and sauger was measured in the field. Sagittal otoliths from freshwater drum and sauger were removed in the field. Scales from river carpsuckers were removed above the lateral line below the dorsal fin insertion (Braaten et al. 1999). In the laboratory, emerald shiners and sicklefin chubs were measured (TL), scales were removed from an area located between the lateral line and dorsal fin insertion (Fuchs 1967; Campbell and MacCrimmon 1970), and mounted between glass slides.

Scales from emerald shiners and sicklefin chubs were viewed under transmitted light, aged, and scale radius and annuli distances measured at 50 X magnification. Otoliths from freshwater drum were sanded along the dorsoventral axis to remove the otolith matrix. Sanding was terminated when the last portion of the otolith matrix had been removed (i.e., at the junction of the otolith matrix and sulcal groove). For age and growth determinations, freshwater drum otoliths were placed in immersion oil and the sanded portion of the otolith was viewed under reflected light. Ages of freshwater drum were determined by counting annuli along the edge of the sulcal groove. Otolith radius

and annuli distances were measured from the nucleus to the otolith edge along the edge of the sulcal groove at 20 X magnification. Scales from small river carpsuckers (e.g., < 80 mm) were mounted between glass slides; whereas, scales from larger river carpsuckers were impressed on acetate slides. River carpsucker scales were aged on a microfiche projector (42 X magnification). Scale radius and annuli distances were measured in the lateral region of the scale (Braaten et al. 1999), and recorded on paper strips. Whole otoliths of sauger were placed in immersion oil and aged under reflected light. Otolith radius and annuli distances were measured at 12.5 X magnification from the nucleus to the tip along the anterior-posterior axis. A dorsovental section of each sauger otolith was used to corroborate ages determined from the whole otolith.

Body structure radius and annuli distances for emerald shiners, sicklefin chubs, freshwater drum, and sauger were digitized directly from the structure using a dissecting microscope interfaced with an image analysis system. Scale radius and annuli distances for river carpsuckers were digitized from paper strips using a light stand interfaced with an image analysis system. No body length corrections to account for preservation effects were applied to emerald shiners and sicklefin chubs.

Two readers independently aged all fish. Each reader measured the radius and annuli distances on a maximum of five scales, or measured the radius and annuli distances on a single otolith. If readers did not agree on an age after two independent aging trials, the fish was omitted. Multiple radius and annuli distances were treated as subsamples and averaged for each individual to obtain a single structure radius and single measurement for each annulus (Pierce et al. 1996).

Life history parameters for emerald shiners, sicklefin chubs, freshwater drum, river carpsucker, and sauger were examined in each segment when sufficient data were available. Longevity (maximum age) was determined by averaging the maximum age of fish collected during the three years of sampling. Mean length at age was estimated by back-calculation. For emerald shiners, sicklefin chubs, and river carpsuckers, the relationship between body length and scale radius was used to determine an a -value (i.e., the intercept) for use in the Fraser-Lee equation (Busacker et al. 1990). A common a -value was estimated by including all segments in the body length - scale radius relationship. Back-calculated length at age and growth increments for freshwater drum and sauger were estimated based on a direct proportion between body length and otolith radius (Tesch 1971). Segment-specific growth trajectories of long-lived species (i.e., freshwater drum, river carpsucker, and sauger) were examined using a von Bertalanffy growth model of the form:

$$L_t = L_{\infty}[1 - e^{-K(t-t_0)}],$$

where L_t is fish length (mm) at age t , L_{∞} is the asymptotic (maximum) length estimate (mm), K is the rate at which L_{∞} is approached (e.g., life-time growth rate), and t_0 is a constant defining the age at which fish length is theoretically zero.

Mean back-calculated length at age-1 (hereafter referred to as the first growth increment) was estimated for the 1995, 1996, and 1997 year classes of emerald shiners, sicklefin chubs, freshwater drum, river carpsucker, and sauger collected in segments. The second growth increment of the 1994, 1995, and 1996 year classes of sicklefin chub, freshwater drum, river carpsucker, and sauger was calculated as the difference between

back-calculated length at age-2 and the first growth increment. Thus, the second growth increment quantified growth that occurred during 1995, 1996, and 1997 for the 1994, 1995, and 1996 year classes. Although earlier year classes were collected in most segments, estimates of the first and second growth increments were restricted to these year classes because 1995 was the earliest period for which water temperature data for several river segments was available, and water temperature data is used in growth rate analysis (see below). Based on age at maturity studies for all species (Carufel 1963; Behmer 1965; Morris 1965; Fuchs 1967; Vasey 1967; Nelson 1968; Campbell and MacCrimmon 1970; Goeman 1983; Bur 1984; Grisak 1996), growth during the first and second growing seasons quantifies growth and growth rate dynamics prior to sexual maturity.

Water Velocity, Water Temperature, and Discharge

Water velocity was measured at all fish sampling locations following standard operating procedures outlined by Sappington et al. (1996, 1998). Water velocity was measured at either 0.6 depth (habitats < 1.2 m) or 0.8 depth and 0.2 depth (habitats > 1.2 m) to obtain an estimate of the average water column velocity used by emerald shiners, sicklefin chubs, freshwater drum, river carpsuckers, and sauger in the habitats where they were collected. For some habitats (e.g., sand bars, secondary channels), a maximum of three velocity measurements were collected and averaged to estimate mean velocity in the habitat. In other habitats (e.g., main channel thalweg), velocity was measured at a single location near the mid-point of the habitat. Habitat-specific water velocities were

averaged for each segment to estimate mean velocity used by emerald shiners, sicklefin chubs, freshwater drum, river carpsuckers, and sauger.

The availability of water temperature data spanning the duration of the growing season was limited in some segments. For segments 3 and 5, daily water temperature data from only the 1997 growing season was obtained (B. Gardner, Montana Department of Fish, Wildlife, and Parks, personal communication). Daily water temperature data for segments 8 and 9 were obtained for 1995-1997 (G. Power, North Dakota Game and Fish Department, personal communication). Data from segment 8 were also used to represent water temperature in segment 7. Daily water temperature for segment 10 (immediately downstream from the junction of segments 8 and 9) was derived for 1995-1997 by averaging daily water temperature from segments 8 and 9. Daily water temperature data for segments 15 and 17 were obtained for the period 1995-1997 (M. Swenson, U.S. Army Corps of Engineers, personal communication), but in some instances data from segment 17 were missing. Missing values were estimated based on a regression relationship between water temperatures measured in segments 15 and 17. In segments 19 - 27, daily water temperature data for 1995-1997 were obtained from several municipalities (e.g., water treatment plants, power plants) that record water temperature at water intake structures. In some instances (e.g., segment 23), water temperature was measured only on a weekly basis. The water temperature recorded at the start of the week was applied to all days in the week. Water temperature data were not obtained for segments 12 or 14. Daily water temperature data in up-river segments (e.g., segment 3, 5, 8, 9) generally

spanned from 1 May to 1 November; whereas, those in lower river segments spanned the calendar year.

For the first growth increment, the growing season was defined as the time period spanning dates when water temperature in each segment first reached spawning temperature to the date when water temperature declined to the minimum temperature for growth. Duration of growth during the second growing season was defined from the first date in the year when water temperature reached the minimum for growth to the last date in the year when water temperature reached the minimum for growth. Due to differences in temperature for spawning and growth, length of the growing season differed between the first and second growth growing seasons.

Determination of spawning temperatures and growing season length was based on published information, and varied among species. Emerald shiners spawn when water temperature exceeds 20°C (Fuchs 1967; Campbell and MacCrimmon 1970). McCormick and Kleiner (1976) found growth of emerald shiners declined sharply as water temperature declined from 16°C to 12°C, but some growth was still evident at 7.0°C. Therefore, initial spawning and minimum growth temperatures for emerald shiners were set at 20°C and 7.0°C, respectively. In the upper Missouri River, Grisak (1996) reported sicklefin chubs spawn at water temperatures 20-23°C, and in the lower Missouri River Tibbs and Galat (1997) inferred spawning temperatures for this species between 22-28°C. No information on minimum growth temperatures is available for sicklefin chubs. Based on this information, spawning initiation temperature was set at 20°C, and 10°C was used to define the minimum growth temperature for sicklefin chubs. The minimum spawning

temperature for freshwater drum is 18°C (Swedberg and Walburg 1970), and the minimum water temperature for growth is 9°C (McInerny and Held 1995). River carpsucker-spawn at 19°C (Fuiman 1982). A water temperature of 10°C was selected as the minimum growth temperature because as no information is available on minimum growth temperatures for river carpsucker. Sauger spawn at 4-14°C (Carufel 1963; Nelson 1968; Walburg 1976; Hokenson 1977), and maintain positive growth rates at water temperatures between 2.9°C and 9.6°C (Wahl and Nielsen 1985). Based on these studies, the minimum spawning temperature was 4°C, and the minimum growth temperature was set at 5°C. Because daily temperature recordings in the upper river segments were initiated when water temperatures were usually greater than 4°C, 1 May was defined as the start of the sauger growing season in all segments.

For each species and growth increment, growing season degree-days were calculated as $\sum(T - T_{\min})$, where T is the recorded daily water temperature (°C) during the specified growing season, and T_{\min} is the minimum growth temperature (°C). Growth rates were expressed as mm/degree-day and mm/day. The mm/degree-day quantifies annual growth increments as a direct function of water temperature during the growing season (Power and McKinley 1997); whereas, mm/day quantifies annual growth as a function of growing season length.

In fishes, growth typically follows a dome-shaped relationship with water temperature where growth rates are maximized at some intermediate temperature range (McCormick and Kleiner 1976). To examine the influence of optimum water temperature on growth, I summed for each segment the number of days in the growing

season where water temperature was in the optimal growth range, and divided the sum by the total number of days in the growing season. This provided an estimate of the percent of the growing season in each segment where water temperature was optimal for growth (i.e., optimal growth frequency; OGF). For emerald shiners, McCormick and Kleiner (1976) found growth rates were maximized between 24°C and 29°C. Hokensen (1977) reported 22°C was the optimum water temperature for growth in sauger. Based on this information, I designated 21°C-23°C as the optimum growth range for sauger. Optimal growth frequency could not be determined for sicklefin chub, river carpsucker, and freshwater drum due to the lack of growth-temperature models.

Discharge data were obtained from U.S. Geological Survey gauging stations located near or within each river segment, and from the U.S. Army Corps of Engineers. Discharge was estimated in some segments. For example, discharge in segment 10 was estimated by averaging discharge data from segments 8 (downstream from Fort Peck dam) and segment 9 (Yellowstone River). Median discharge (m³/s) during the growing season (based on water temperature described above) was used to characterize flow regimes in river segments.

Statistical Analyses

Statistical analyses were conducted using SAS (1990). Relationships between life history parameters (i.e., mean maximum age, mean length at age, K , L_{∞} ; dependent variables), and latitude (° North), mean water temperature (°C), and degree-days (independent variables) were examined using linear and nonlinear regression analyses. Linear and nonlinear regression was used to examine relationships between growth of

emerald shiners, freshwater drum, river carpsucker, and sauger during the first and second growing seasons (i.e., mm, mm/degree-day, mm/day; dependent variables) and latitude (independent variable). Statistical significance of nonlinear regression models was based on model r^2 - values and parameter estimates (e.g., P - values ≤ 0.05). Because sicklefin chubs were infrequently sampled, particularly in mid-latitude segments, analysis of variance (ANOVA) was used to compare growth increments and growth rates of this species among latitudes. Sample sizes for the regressions involving growth increments differed from those involving growth rates because water temperature data were not available for all segments and year classes. Latitudes were omitted from the analyses if the sample size for an individual year class was one. Regression analysis was used to examine relationships between growth increments and growth rates (dependent variables) during the first growing season and mean water velocity used during the first growing season (independent variable). Correlation analysis was used to examine associations between growth rates and OGF.

The first and second growth increments from back-calculations were used to examine relationships between growth and median discharge during the growing season within segments. Back-calculated lengths and increments were examined for Lee's phenomenon by examining bivariate plots of growth increments (y-axis) versus year class (x-axis). A consistent positive trend (e.g., growth increments increase as year class increases) would suggest Lee's phenomenon, unless the environmental factor (in this case river discharge) similarly increased with respect to year class, and the growth increment linearly increased with increasing discharge. To examine this possibility, bivariate plots

of back-calculated growth increments versus body structure increment were examined for deviations from linearity. The first and second growth increments of emerald shiner, sicklefin chub, freshwater drum, river carpsucker, and sauger were compared among year classes within segments using a one-way ANOVA. When growth increments differed significantly among year classes ($P < 0.05$), linear or nonlinear regression was used to examine relationships between the first and second growth increments of species in each segment (dependent variables), and segment-level median discharge during the growing season (independent variable). For those year classes where water temperature data were not available, the start and end of the growing season was estimated based on years when water temperature data were available. Assumptions of parametric analyses were tested with Levene's test for homogeneity of variances (Milliken and Johnson 1992), and the Shapiro-Wilk test for normality (SAS 1990).

Results

Latitudinal Variations in Growth

Water Temperature

Water temperature and duration of the growing season among segments followed patterns consistent with latitudinal variation in thermal conditions. River segment was inversely correlated with latitude ($r = -0.95$, $P = 0.0001$, $N = 17$); thus, latitude was used to quantify segments. Mean water temperature, degree-days, and number of days in the growing season for segments were inversely correlated with latitude for all species (Table 1). Averaged across species, mean water temperature and number of days in the growing

Table 1.-Correlation coefficients between latitude and mean water temperature (°C), degree-days, and number of days in the growing season (number of days) for emerald shiner, sicklefin chub, freshwater drum, river carpsucker, and sauger. Sample size for each correlation are in parentheses. Minimum and maximum values for each variable are hyphenated. Probability values for all correlations are $P < 0.002$.

Species	Mean water temperature (°C)	Degree-days	Number of days
Emerald shiner	-0.91 (13) 16-21	-0.97 (13) 1,135-2,459	-0.96 (13) 121-175
Sicklefin chub	-0.97 (8) 17-22	-0.97 (8) 889-2,150	-0.90 (8) 121-175
Freshwater drum	-0.97 (7) 19-22	-0.99 (7) 1,379-2,180	-0.95 (7) 144-175
River carpsucker	-0.94 (11) 17-22	-0.98 (11) 834-1,965	-0.93 (11) 113-175
Sauger	-0.93 (11) 16-20	-0.97 (11) 2,035-3,100	-0.92 (11) 177-210

season were 1.3 times greater in the southern than northern latitudes. Degree-days averaged 2.0 times greater in the southern than northern latitudes.

Life History Parameters

Longevity.-Maximum age of emerald shiners, sicklefin chubs, river carpsuckers, and saugers varied among species and latitude (Figure 2). An asymptotic model provided the strongest relationship between maximum age and latitude for emerald shiners, and indicated maximum age increased from low latitudes (e.g., segments 25 and 27) to mid-latitudes (segment 18), then remained unchanged at high-latitudes. Maximum age of sicklefin chubs was significantly correlated with latitude, and curvilinearly increased from low to high latitudes. Maximum age and latitude were linearly correlated for river carpsuckers and sauger. Maximum age of freshwater drum was not significantly related to latitude ($r^2 = 0.18$, $P = 0.08$, $N = 17$).

Growth patterns.-Growth of freshwater drum, river carpsuckers, and sauger followed von Bertalanffy growth trajectories. Growth of freshwater drum was highly variable among segments (Figure 3). After age-1, growth diverged among segments and was rapid in segments 19 and 22 but slow in segments 3 and 5. The growth coefficient (K) varied from 0.10 to 0.42, and L_{∞} from 354 mm to 519 mm (Table 2). There were no significant relationships between von Bertalanffy parameters and latitude, mean water temperature, degree-days, and the number of days in the growing season (P -values > 0.19) for freshwater drum, although there was a positive trend between K and mean water temperature ($r^2 = 0.46$, $P = 0.06$, $N = 8$).

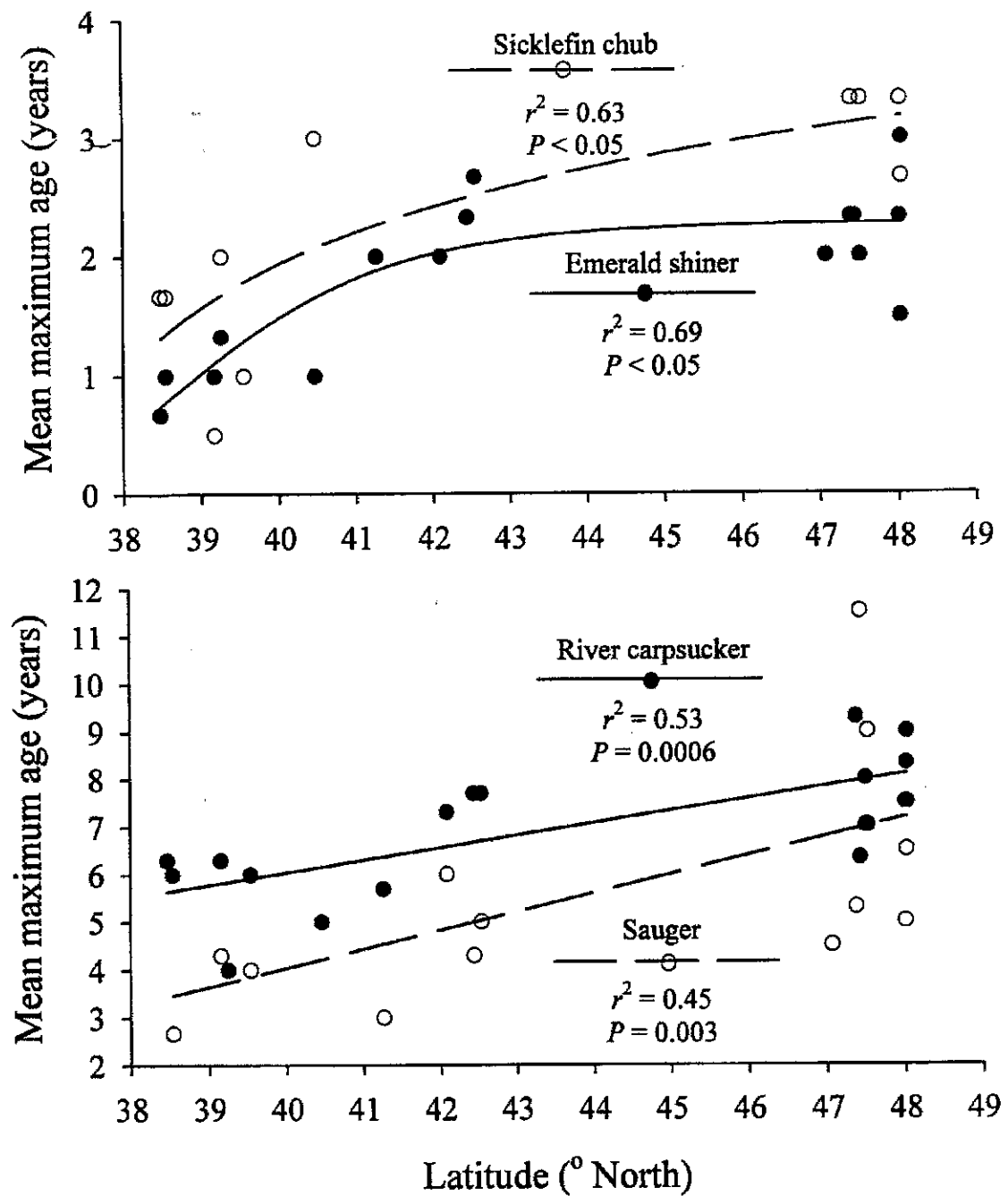


Figure 2.-Relations between mean maximum age (years) and latitude (° North) for emerald shiners and sicklefin chub (top panel), and river carpsucker and sauger (lower panel).

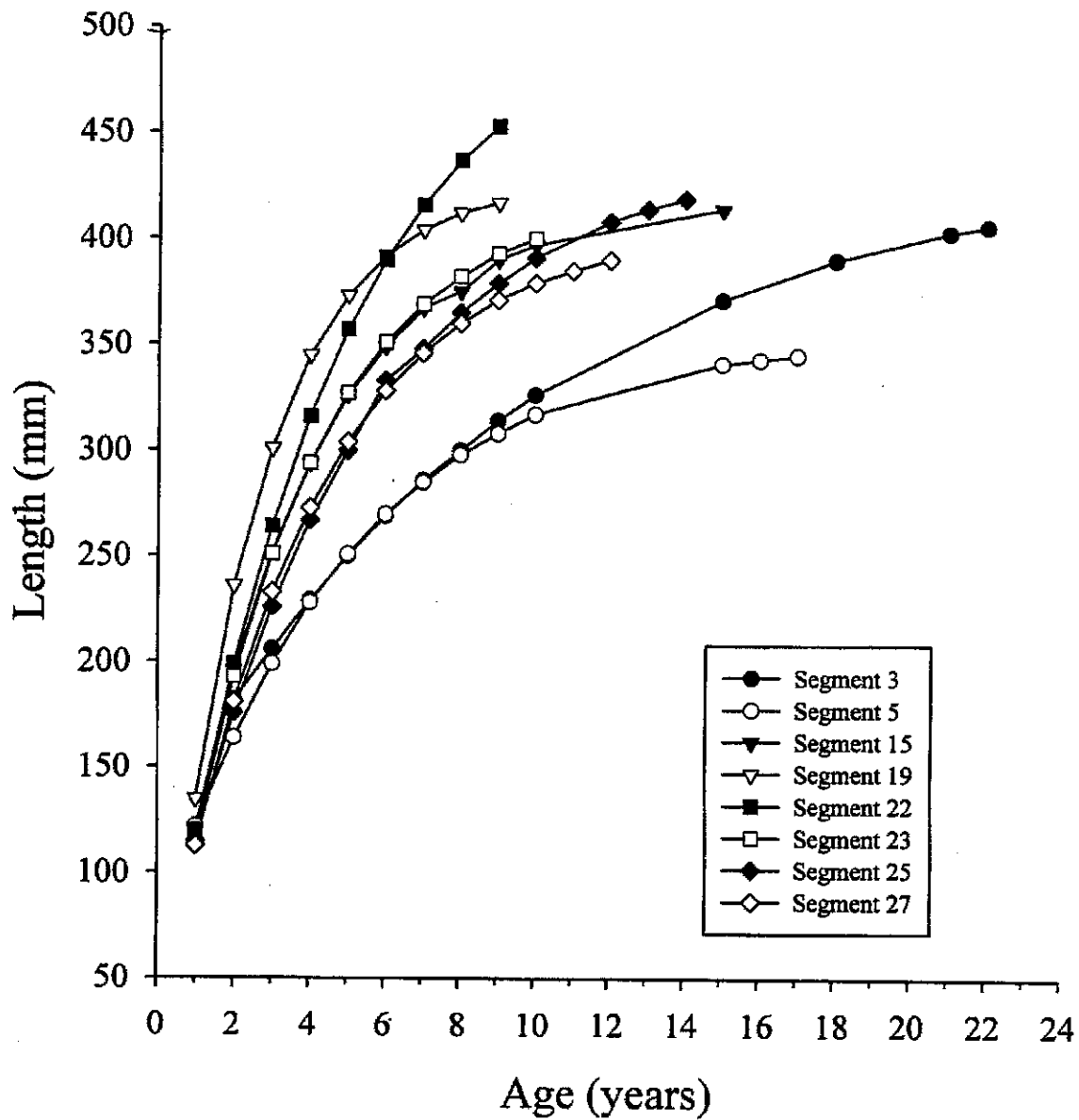


Figure 3.-Growth trajectories using a von Bertalanffy growth model by segment for freshwater drum sampled in the Missouri River from 1996 - 1998.

Table 2.-Growth model parameters (L_{∞} , K , t_0), 95% confidence intervals (in parentheses), and model r^2 -values by segment for freshwater drum sampled in the Missouri River during 1996 - 1998.

Segment	r^2	L_{∞} (mm)	K	t_0
3	0.86	439 (393-485)	0.10 (0.07-0.13)	-3.17 (-4.28--2.08)
5	0.86	354 (329-379)	0.20 (0.15-0.25)	-1.08 (-1.77--0.41)
15	0.73	419 (371-467)	0.29 (0.17-0.41)	-0.19 (-0.94-0.56)
19	0.94	427 (387-468)	0.42 (0.24-0.60)	0.10 (-0.34-0.54)
22	0.92	519 (401-637)	0.23 (0.10-0.35)	-0.14 (-0.65-0.36)
23	0.93	422 (377-467)	0.29 (0.21- 0.38)	-0.09 (-0.43-0.26)
25	0.93	441 (396-485)	0.21 (0.16-0.26)	-0.45 (-0.82--0.08)
27	0.90	406 (370-443)	0.26 (0.20-0.33)	-0.23 (-0.58-0.12)

Growth trajectories of river carpsuckers were similar among segments between ages 2 and 5, then diverged at older ages (Figure 4). Estimates of K varied from 0.14 to 0.37 and L_{∞} varied from 451 mm to 675 mm (Table 3). The growth coefficient (K) of river carpsuckers was inversely related to latitude, and positively related to mean water temperature, degree-days, and the number of days in the growing season (Table 4). There were no significant relations between L_{∞} and latitude, mean water temperature, degree-days, and the number of days in the growing season for river carpsuckers (P -values > 0.18). There was a significant inverse correlation between K and L_{∞} for river carpsuckers ($r = -0.76$, $P = 0.003$, $N = 13$).

Sauger growth trajectories varied greatly among segments (Figure 5). Growth was rapid at low latitudes (segments 15, 17, 19), but slower at higher latitudes (3, 5, 8, 10). Across all segments, L_{∞} varied from 482 mm to 750 mm, and K from 0.11 to 0.55 (Table 5). For sauger, K was inversely related to latitude, but positively related to mean water temperature and degree-days (Table 4). Asymptotic length (L_{∞}) of sauger was not significantly related to latitude, mean water temperature, degree-days, and the number of days in the growing season (P -values > 0.23). There was a significant inverse correlation between K and L_{∞} ($r = -0.70$, $P = 0.05$, $N = 8$).

Mean length at age.-Correlations between mean back-calculated length at age and latitude varied among species (Figure 6). Mean back-calculated length at ages-1 and 2 of emerald shiners and sicklefin chubs were not significantly correlated with latitude. Emerald shiners and sicklefin chubs older than age-2 were infrequently sampled in the majority of segments which prevented analyses of older age classes. Mean back-

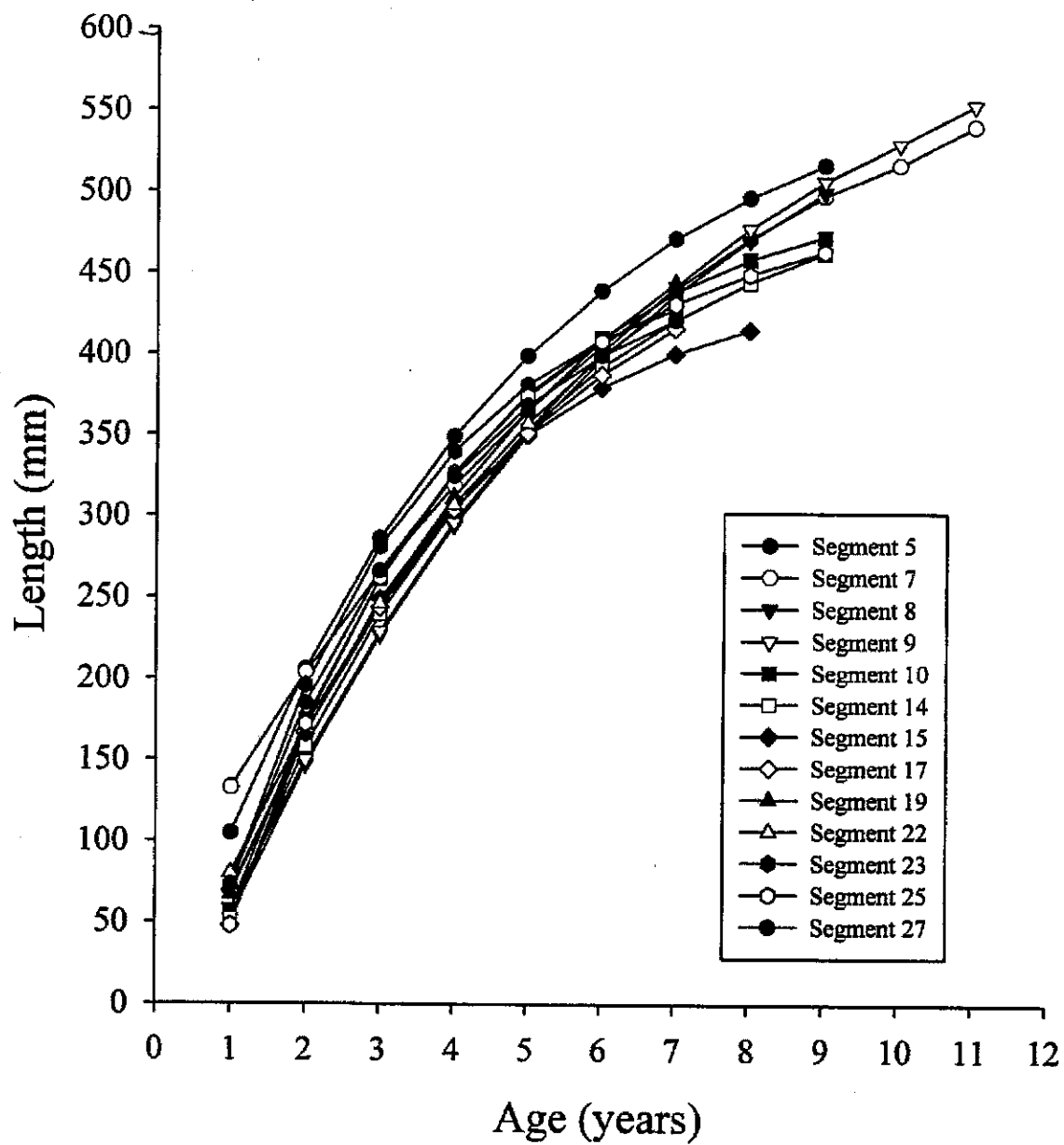


Figure 4.-Growth trajectories using a von Bertalanffy growth model by segment for river carpsuckers sampled the Missouri River and Yellowstone River during 1996 - 1998.

Table 3.-Growth model parameters (L_{∞} , K , t_0), 95% confidence intervals (in parentheses), and model r^2 -values by segment for river carpsuckers sampled in the Missouri River and Yellowstone River during 1996 - 1998.

Segment	r^2	Growth model parameters		
		L_{∞} (mm)	K	t_0
5	0.90	593 (484-702)	0.23 (0.12-0.34)	0.15 (-0.49-0.79)
7	0.77	669 (520-818)	0.14 (0.08-0.21)	-0.56 (-1.33-0.22)
8	0.91	646 (513-779)	0.17 (0.11-0.24)	0.51 (0.18-0.85)
9	0.92	675 (563-786)	0.16 (0.12-0.21)	0.45 (0.26-0.65)
10	0.97	514 (393-635)	0.30 (0.14-0.45)	0.61 (0.36-0.86)
14	0.90	523 (470-577)	0.26 (0.20-0.32)	0.59 (0.37-0.82)
15	0.80	451 (416-486)	0.35 (0.28-0.41)	0.68 (0.49-0.86)
17	0.87	516 (395-637)	0.25 (0.13-0.37)	0.43 (0.06-0.79)
19	0.94	603 (427-778)	0.20 (0.11-0.30)	0.42 (0.23-0.61)
22	0.91	587 (444-731)	0.20 (0.11-0.28)	0.26 (-0.01-0.53)
23	0.87	473 (391-554)	0.37 (0.19-0.54)	0.54 (0.19-0.89)
25	0.86	497 (392-601)	0.32 (0.18-0.47)	0.69 (0.39-0.99)
27	0.77	480 (366-595)	0.32 (0.12-0.52)	0.49 (-0.12-1.10)

Table 4. -Significant regression relationships ($P < 0.05$) between von Bertalanffy growth parameter K and latitude, mean water temperature ($^{\circ}\text{C}$), degree-days, and total number of days in the growing season for river carpsucker and sauger sampled in the Missouri River and Yellowstone River during 1996 - 1998.

Species	Model	r^2	P	N
River carpsucker	$K = -0.011 (^{\circ}\text{ North}) + 0.71$	0.31	0.05	13
	$K = 0.031 (\text{mean water temperature}) - 0.33$	0.38	0.03	12
	$K = 0.0001 (\text{degree-days}) + 0.06$	0.34	0.05	12
	$K = 0.002 (\text{total days}) - 0.18$	0.34	0.05	12
Sauger	$K = -0.04 (^{\circ}\text{ North}) + 2.29$	0.75	0.005	8
	$K = 0.12 (\text{mean water temperature, } ^{\circ}\text{C}) - 1.75$	0.67	0.02	7
	$K = 0.0004 (\text{degree-days}) - 0.56$	0.60	0.04	7

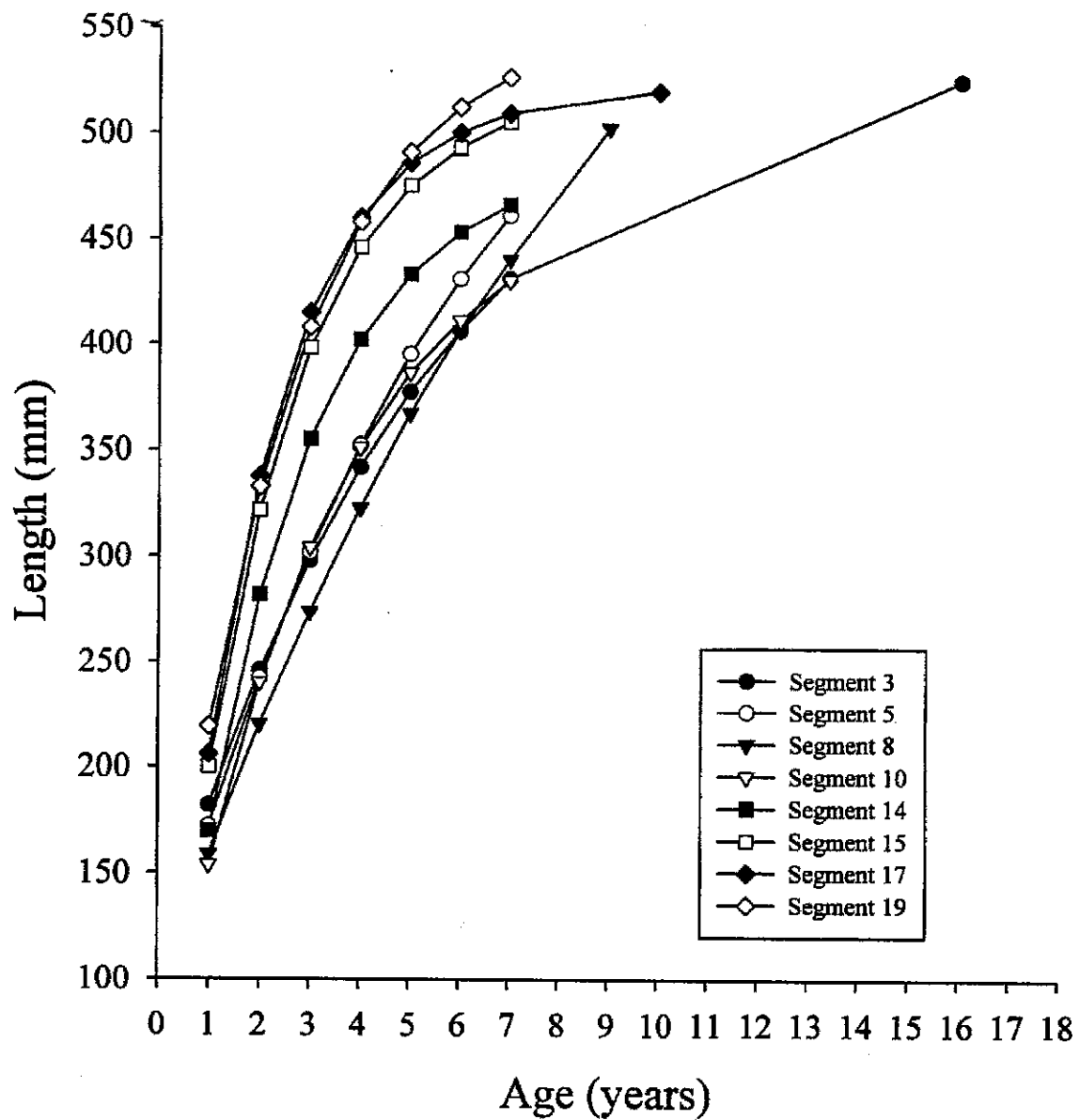


Figure 5.-Growth trajectories using a von Bertalanffy growth model by segment for sauger sampled in the Missouri River from 1996 - 1998.

Table 5.-Growth model parameters (L_{∞} , K , t_0), 95% confidence intervals (in parentheses), and model r^2 -values by segment for sauger sampled in the Missouri River during 1996 - 1998.

Segment	r^2	L_{∞} (mm)	K	t_0
3	0.87	543 (446-640)	0.19 (0.10-0.29)	-1.09 (-2.07--0.11)
5	0.87	629 (625-933)	0.17 (0-0.34)	-0.92 (-2.03--0.20)
8	0.90	750 (251-1,249)	0.11 (0-0.23)	-1.19 (-2.50-0.11)
10	0.92	482 (395-569)	0.31 (0.16-0.46)	-0.26 (-0.75-0.24)
14	0.91	490 (410-569)	0.43 (0.21-0.66)	-0.01 (-0.53-0.56)
15	0.95	523 (464-583)	0.48 (0.30-0.66)	-0.01 (-0.23-0.21)
17	0.90	521 (460-583)	0.55 (0.29-0.80)	0.08 (-0.31-0.47)
19	0.93	554 (453-656)	0.42 (0.13-0.70)	-0.21 (-0.82-0.40)

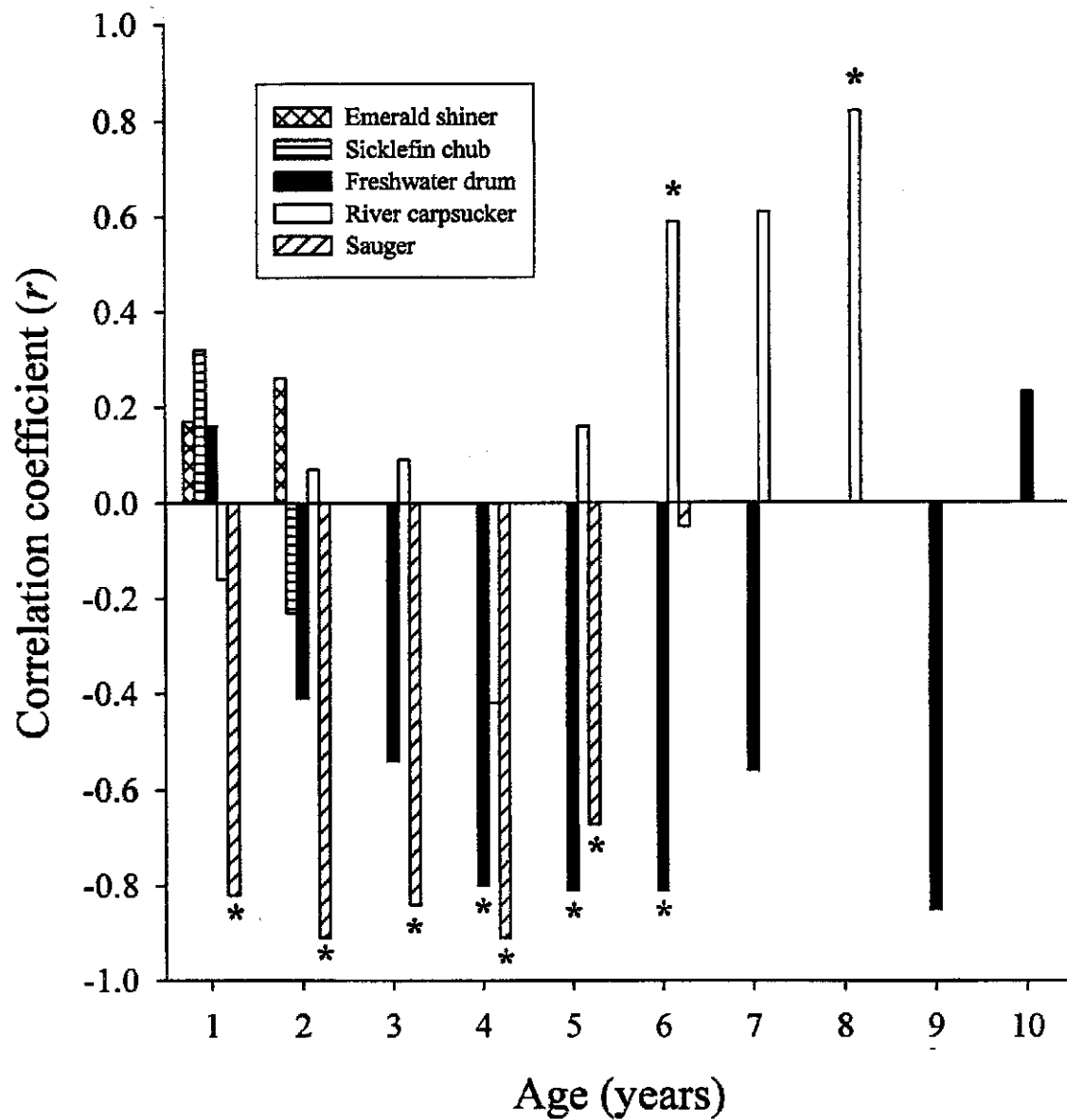


Figure 6.-Linear correlation coefficients by age for the relationship between mean back-calculated length at age and latitude for emerald shiners, sicklefin chubs, freshwater drum, river carpsuckers, and sauger. Asterisks represent correlations with P -values < 0.05 .

calculated length of freshwater drum at ages 4 - 6 were inversely related to latitude, and there was some indication that this inverse trend was maintained at older ages (e.g., age-9, $r = -0.85$; $P = 0.07$). There were significant positive relationships between mean back-calculated length of river carpsuckers at ages-6 and 8, and evidence for a similar trend at age-7 ($r = 0.61$, $P = 0.09$). Mean back-calculated length of sauger at ages 1 - 5 was inversely related to latitude. Due to the short life span of sauger in lower latitudes, correlations for age-6 sauger only included latitudes from upper segments (i.e., 3, 7, 8, 9, 10).

Growth Increments and Growth Rates During the First and Second Growing Seasons

For all species, growth increments attained during the first and second growing seasons were positively correlated with growth rate (Table 6). Growth increments during the first growing season were significantly correlated (r -values > 0.56) with mm/day for all species, but growth of only sicklefin chub was significantly correlated with mm/degree-day. Similarly, the second growth increment of sicklefin chub, freshwater drum, river carpsucker, and sauger was significantly correlated with mm/day (Table 6); whereas, mm/degree-day was correlated with the second growth increment for river carpsuckers and sauger (Table 6). Both growth rate estimates were highly correlated (r -values > 0.51) for all species, except for river carpsuckers during the first growing season.

Emerald shiner. -A quadratic model indicated the first growth increment of emerald shiners was smallest in the lowest latitude (segment 27), increased through mid-latitudes (segment 14), then declined at higher latitudes (segments 7 and 8; Figure 7). Growth rate (mm/degree-day) was positively related to latitude (Figure 7), and growth

Table 6.-Correlation coefficients for relationships between growth increment (mm) and growth rate (mm/degree-day, mm/day) for emerald shiners, sicklefin chubs, freshwater drum, river carpsuckers, and sauger during the first and second growing seasons. Asterisks denote P -values ≤ 0.05 . Sample size is shown in parentheses.

Correlation variables		Species				
		Emerald shiner	Sicklefin chub	Freshwater drum	River carpsucker	Sauger
First-year growth						
Increment	mm/degree-day	0.35 (28)	0.75* (15)	0.44 (13)	-0.14 (22)	0.30 (20)
Increment	mm/day	0.56* (28)	0.76* (15)	0.85* (13)	0.71* (22)	0.91* (20)
Mm/degree-day	mm/day	0.89* (28)	0.98* (15)	0.80* (13)	0.44* (22)	0.51* (20)
Second-year growth						
Increment	mm/degree-day		0.33 (11)	0.42 (15)	0.46* (25)	0.69* (18)
Increment	mm/day		0.73* (11)	0.82* (15)	0.76* (25)	0.96* (18)
Mm/degree-day	mm/day		0.69* (11)	0.84* (15)	0.79* (25)	0.76* (18)

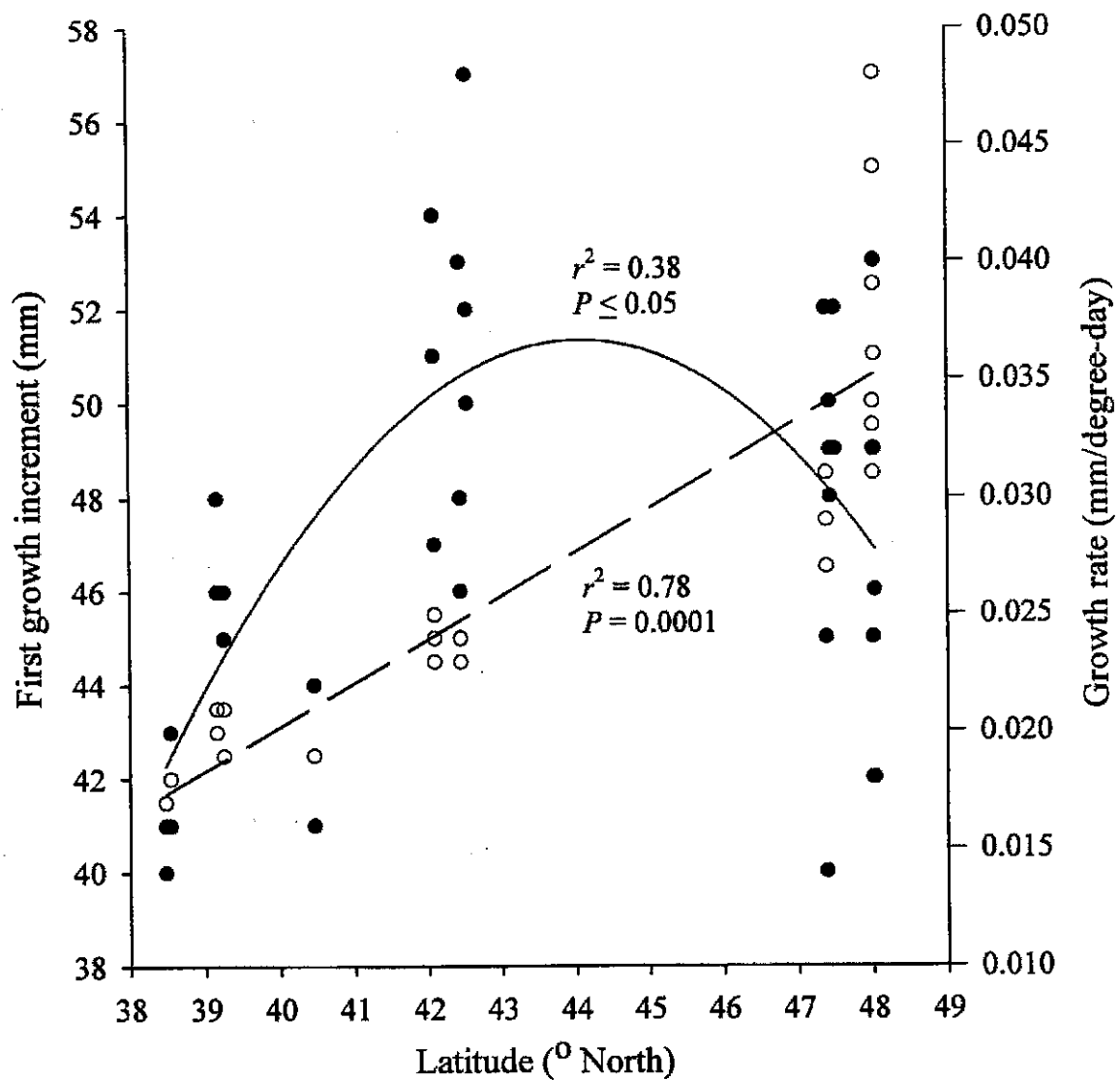


Figure 7.-Relations between the first growth increment (mm; solid line and solid circles) and growth rate (mm/degree-day; dashed line and open circles) and latitude (° North) for emerald shiners sampled in the Missouri River and Yellowstone River during 1996 - 1998.

rate expressed as mm/day was also positively related to latitude ($r^2 = 0.58$, $P = 0.0001$, $N = 28$). The first growth increment of emerald shiners was positively related to water velocity ($r^2 = 0.27$, $P = 0.027$, $N = 18$; velocity 0 - 0.48 m/s), but there were no significant relationships between water velocity and mm/degree-day ($r^2 = 0$, $P = 0.89$, $N = 18$) and mm/day ($r^2 = 0.01$, $P = 0.65$, $N = 18$). There was no significant correlation between latitude and water velocity used by emerald shiner ($r = 0.02$, $P = 0.95$, $N = 18$).

Sicklefin chub.—The first growth increment of sicklefin chubs did not differ significantly among latitudes ($F = 1.89$, $df = 5, 9$, $P = 0.19$), and averaged 38 mm ($38^\circ 47'$), 40 mm ($38^\circ 54'$), 41 mm ($47^\circ 38'$), 41 mm ($47^\circ 50'$), 38 mm ($48^\circ 01'$), and 44 mm ($48^\circ 03'$). Growth rate (mm/degree-day) differed significantly among latitudes ($F = 13.21$, $df = 4, 7$, $P = 0.002$). Mean growth rate was significantly greater ($P < 0.05$) at high latitudes ($48^\circ 03' = 0.051$ mm/degree-day, $48^\circ 01' = 0.038$ mm/degree-day, $47^\circ 38' = 0.034$ mm/degree-day) than low latitudes ($38^\circ 47' = 0.018$ mm/degree-day, $38^\circ 54' = 0.02$ mm/degree-day). Mean growth rate expressed as mm/day also differed significantly among latitudes ($F = 6.91$, $df = 4, 7$, $P = 0.014$), and followed a pattern similar to mm/degree-day where mm/day was significantly greater ($P < 0.05$) at $48^\circ 03'$ (mean = 0.37 mm/day) than at $38^\circ 47'$ (mean = 0.21 mm/day). The first growth increment was not significantly related to water velocity ($r^2 = 0.07$, $P = 0.91$, $N = 5$; velocity 0 - 1.06 m/s). Growth rate was not significantly related to water velocity, but there was evidence that mm/degree-day ($r^2 = 0.68$, $P = 0.09$, $N = 5$) and mm/day ($r^2 = 0.74$, $P = 0.06$, $N = 5$) were positively related to water velocity. Latitude and water velocity used by sicklefin chub were marginally correlated ($r = 0.86$, $P = 0.06$, $N = 5$).

For sicklefin chub during the second growing season, there were no significant differences in growth increments among latitudes ($F = 1.9$, $df = 4, 9$, $P = 0.19$). Mean growth increments during the second growing season were 36 mm ($38^{\circ} 54'$), 31 mm ($47^{\circ} 38'$), 28 mm ($47^{\circ} 05'$), 32 mm ($48^{\circ} 01'$), and 32 mm ($48^{\circ} 03'$). Mean growth rate expressed as mm/degree-day did not differ significantly among latitudes ($F = 1.9$, $df = 2, 6$, $P = 0.23$), and was 0.023 mm/degree-day ($47^{\circ} 38'$), 0.026 mm/degree-day ($48^{\circ} 01'$), and 0.029 mm/degree-day ($48^{\circ} 03'$). Mean growth rate expressed as mm/day did not differ significantly among latitudes ($F = 0.0$, $df = 2, 6$, $P = 0.99$), and was 0.183 ($48^{\circ} 03'$), 0.185 ($48^{\circ} 01'$), and 0.185 ($47^{\circ} 38'$).

Freshwater drum.-The 1995 - 1997 year classes of freshwater drum were infrequently sampled in mid-latitude segments which hindered statistical analyses (Figure 8). The first growth increment generally increased from the lowest latitudes to a maximum near 41° North (segment 19), then declined through segment 15 and higher latitudes. Growth rate (mm/degree-day) of freshwater drum during the first growing season was positively related to latitude (Figure 8), and mm/day exhibited a relationship with latitude similar to the first growth increment. The first growth increment was positively related to water velocity ($r^2 = 0.68$, $P = 0.02$, $N = 7$; velocity 0.07 - 0.40 m/s). There were significant positive relationships between water velocity and mm/degree-day ($r^2 = 0.78$, $P = 0.009$, $N = 7$) and mm/day ($r^2 = 0.76$, $P = 0.011$, $N = 7$). Latitude and water velocity used by freshwater drum were not significantly correlated ($r = 0.41$, $P = 0.36$, $N = 7$).

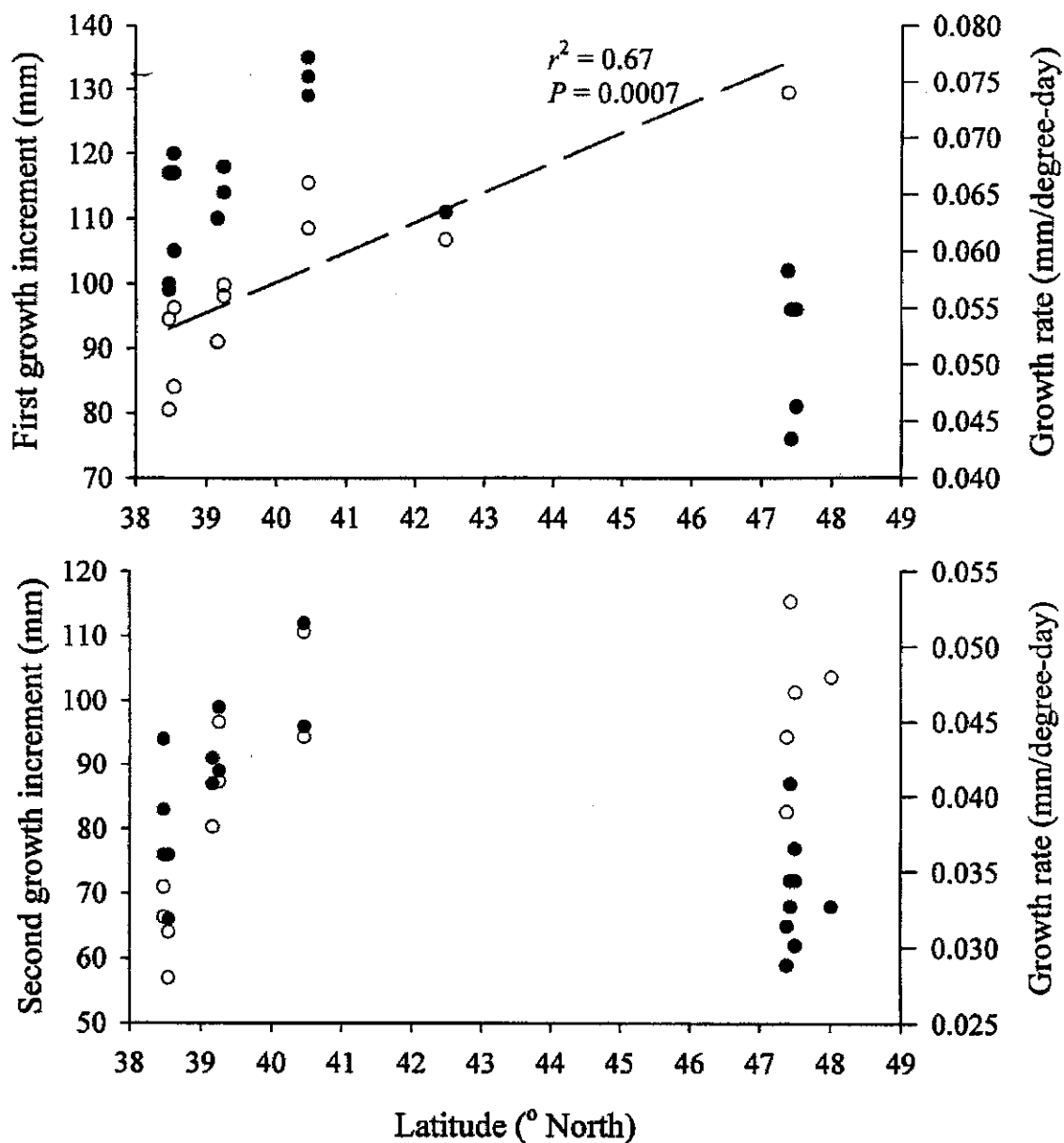


Figure 8.-Relations between the first and second growth increment (mm; solid circles) and growth rate (mm/degree-day; dashed line and open circles) and latitude (° North) for freshwater drum sampled in the Missouri River and Yellowstone River during 1996 - 1998.

Age-2 freshwater drum were infrequently collected in mid-latitude segments (Figure 8). Similar to the first growth increment, the second growth increment of freshwater drum generally increased from low latitudes (e.g., segment 25, 27) to a maximum near mid-latitudes (segment 19), then declined through higher latitudes (Figure 8). Growth rate (mm/degree-day) during the second growing season also increased from lower latitudes to a maximum at 40.46° North, then remained high at higher latitudes. Growth rate expressed as mm/day followed a pattern similar to the second growth increment.

River carpsucker.-The first growth increment of river carpsuckers was inversely related to latitude (Figure 9). In this analysis, growth increments from segments 7 (101 mm) and 9 (81 mm) at the higher latitudes generally exceeded growth increments from other high-latitude segments. Based on influence diagnostics (i.e., studentized residuals, dffits, press statistic; SAS 1991), the growth increment from segment 7 was omitted from the analysis. Growth rate (mm/degree-day) during the first growing season was positively related to latitude (Figure 9), but there was no significant relationship between mm/day and latitude ($r^2 = 0.02$, $P = 0.55$, $N = 22$). There was no significant relationship between the first growth increment and water velocity ($r^2 = 0.19$, $P = 0.14$, $N = 13$; velocity 0 - 0.26 m/s). Although mm/degree-day was not significantly related to water velocity ($r^2 = 0.14$, $P = 0.20$, $N = 13$), there was a significant inverse relationship between mm/day and velocity ($r^2 = 0.58$, $P = 0.003$, $N = 13$). There was no significant correlation between latitude and water velocity used by river carpsuckers ($r = 0.01$, $P = 0.97$, $N = 13$).

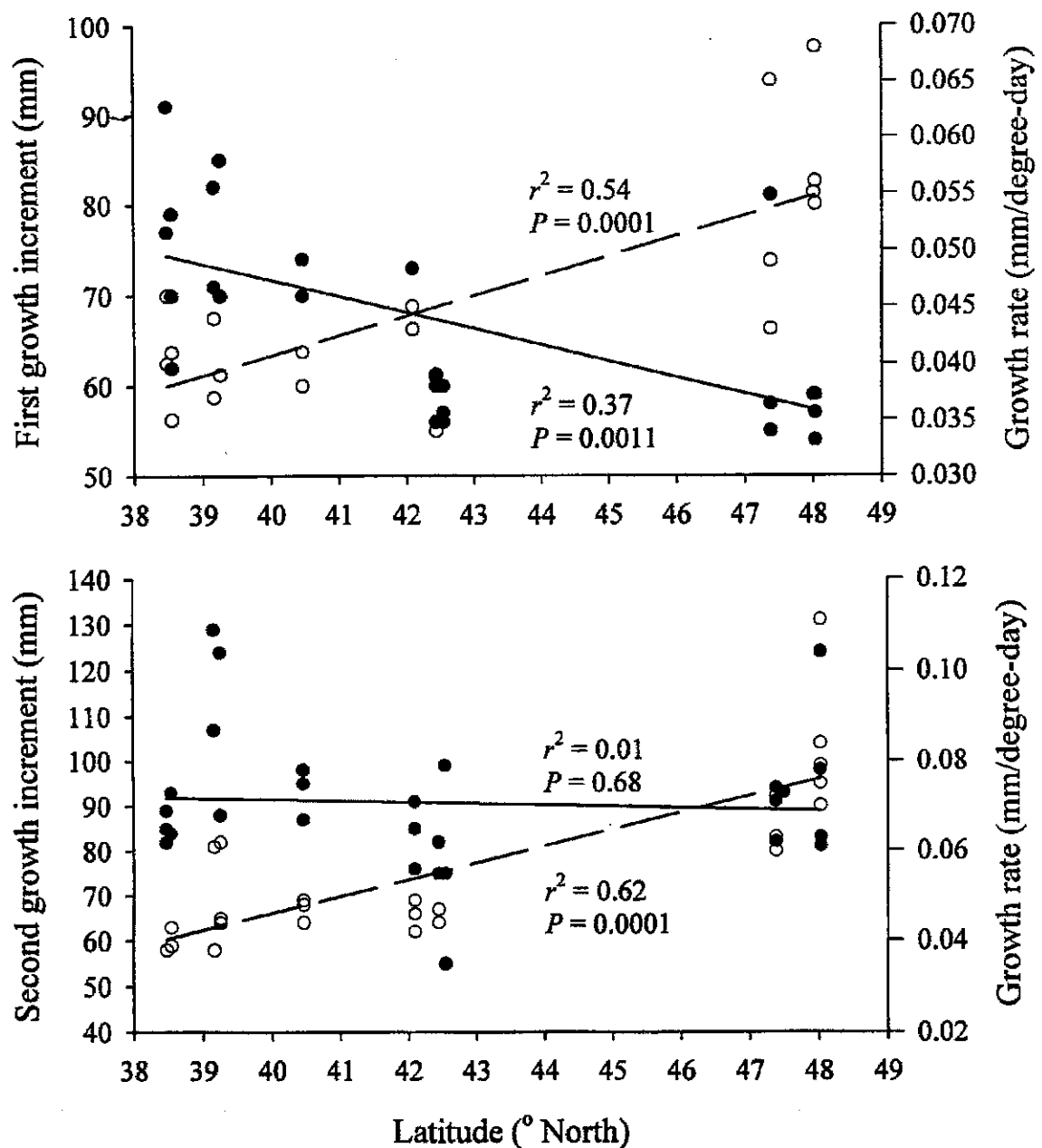


Figure 9.-Relations between the first and second growth increment (mm; solid line and solid circles) and growth rate (mm/degree-day; dashed line and open circles) and latitude (° North) for river carpsuckers sampled in the Missouri River and Yellowstone River during 1996 - 1998.

The second growth increment of river carpsuckers was not significantly related to latitude, but mm/degree-day was positively related to latitude (Figure 9). Growth rate expressed as mm/day was also positively related to latitude for river carpsuckers ($r^2 = 0.22$, $P = 0.018$, $N = 25$).

Sauger.-The first growth increment of sauger was negatively related to latitude (Figure 10). Although there was no relationship between mm/degree-day and latitude ($r^2 = 0.03$, $P = 0.49$, $N = 20$), growth rate expressed as mm/day was inversely related to latitude (Figure 10). There was no significant relationship between the first growth increment and water velocity ($r^2 = 0.24$, $P = 0.09$, $N = 13$; velocity = 0 - 0.80 m/s), but mm/degree-day ($r^2 = 0.33$, $P = 0.04$, $N = 13$) and mm/day ($r^2 = 0.33$, $P = 0.04$, $N = 13$) were positively related to water velocity. Lack of a correlation between latitude and water velocity used by sauger ($r = -0.15$, $P = 0.62$, $N = 13$) facilitated development of a multiple regression model for sauger growth rate: mm/day = -0.019 ($^{\circ}$ North) + 0.23 (mean velocity, m/s) + 1.75 . The overall model was significant ($R^2 = 0.69$, $P = 0.003$, $N = 13$), and all model parameters were significantly different from zero (P -values < 0.02).

The second growth increment of sauger was inversely related to latitude (Figure 10). Growth rate expressed as mm/degree-day was not significantly related to latitude ($r^2 = 0.13$, $P = 0.15$, $N = 18$), but mm/day was inversely related to latitude (Figure 10).

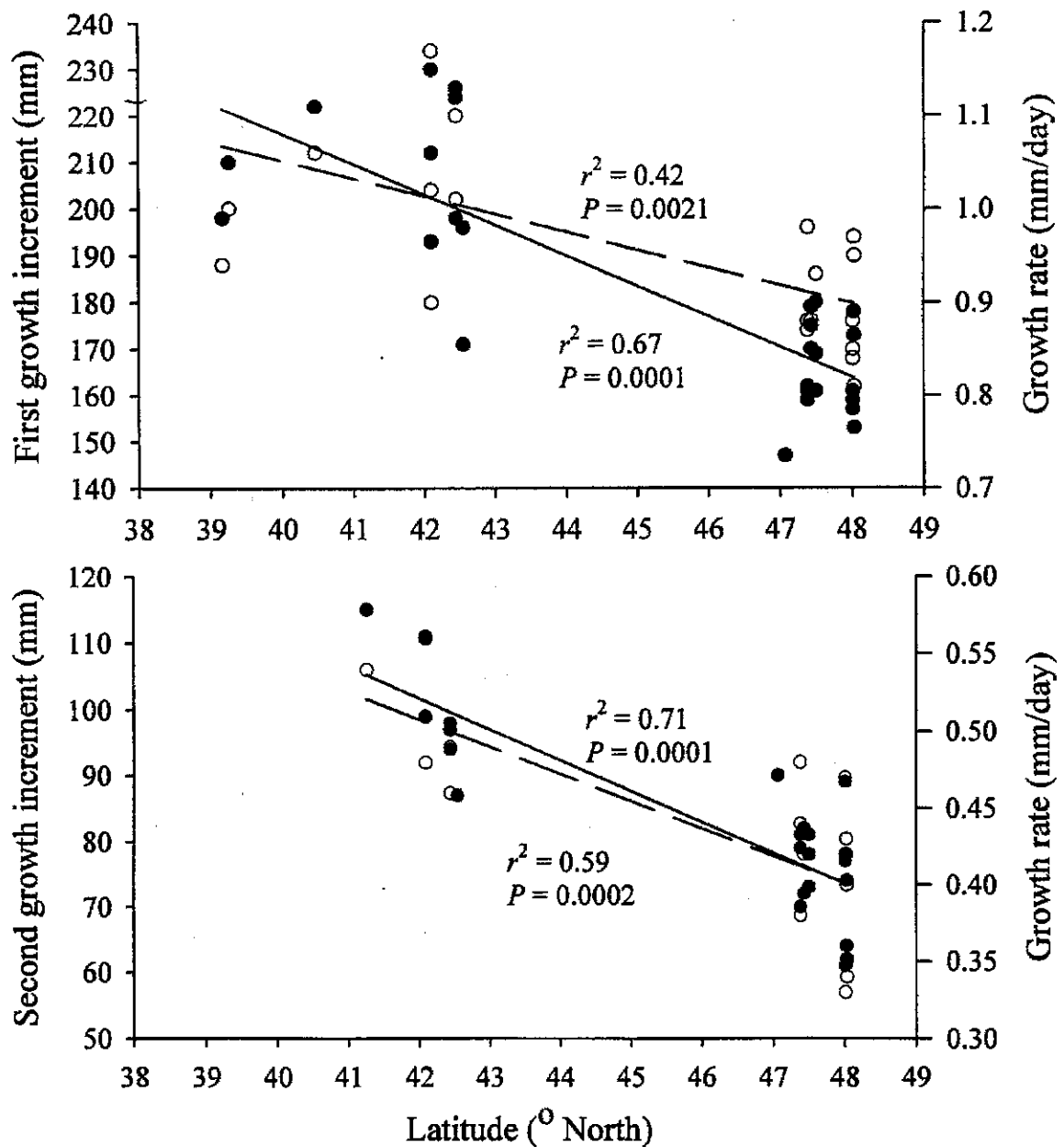


Figure 10.-Relations between the first and second growth increment (mm; solid line and solid circles) and growth rate (mm/day; dashed line and open circles) and latitude (° North) for sauger sampled in the Missouri River and Yellowstone River during 1996 - 1998.

Growth Rate Related to Optimal Growth Frequency

Emerald shiner.-For the 1995 - 1997 year classes of emerald shiners, the number of days where water temperature was optimal for growth (i.e., 24°C - 29°C) varied from zero at some high latitudes (e.g., segments 7, 8, 10) to 69 - 88 days at low latitudes (e.g., segments 23 - 27). As a consequence, OGF varied from zero to 53% of the growing season and was inversely correlated with latitude ($r = -0.93$, $P = 0.0001$, $N = 28$). There were significant inverse correlations between OGF and mm/degree-day ($r = -0.84$, $P = 0.0001$, $N = 28$) and between OGF and mm/day ($r = -0.66$, $P = 0.0001$, $N = 28$).

Sauger.-The number of days where water temperature was optimal for growth (i.e., 21°C - 23°C) for the 1995 - 1997 year classes of sauger varied from eight in southern latitudes (e.g., segment 22) to 50 days in northern latitudes (e.g., segment 9). Optimal growth frequency varied from 4% to 27% of the growing season, and was positively correlated with latitude ($r = 0.54$, $P = 0.01$, $N = 20$). There were no significant correlations between OGF and mm/degree-day ($r = -0.03$, $P = 0.91$, $N = 20$) and between OGF and mm/day ($r = -0.35$, $P = 0.13$, $N = 20$).

Segment-level Growth Response to Discharge

Emerald shiners

The first growth increment of emerald shiners differed significantly among year classes in 7 of 14 segments (Table 7). Due to the short life span of emerald shiners, regressions between growth and discharge were limited. There were no significant relations (r^2 -values 0 - 0.16, P -values 0.60-0.99) between growth increments and median

Table 7.-Mean first-year growth increments (mm; standard error and sample size in parentheses) of the 1994-1997 year classes of emerald shiners in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class			
		1994	1995	1996	1997
3	0.22	52 (3.0,5)	50 (0.9,38)	48 (0.6,85)	49 (0.8,67)
5	0.0001	52 ^{a,b} (2.5,3)	52 ^a (0.8,107)	49 ^b (0.5,112)	49 ^b (0.5,134)
7	0.39			49 (2.4,10)	46 (1.1,18)
8	0.02			53 ^a (1.6,2)	42 ^b (1.9,10)
9	0.0001		52 ^a (1.1,3)	40 ^b (0.7,50)	45 ^b (0.7,97)
10	0.02		49 ^a (2.0,6)	42 ^b (1.4,24)	45 ^{a,b} (1.1,28)
14	0.0001	49 ^b (2.9,3)	52 ^{a,b} (1.6,32)	57 ^a (0.7,133)	50 ^{a,b} (0.9,65)
15	0.0001	48 ^b (1.4,14)	53 ^a (1.2,34)	46 ^b (0.5,323)	48 ^b (0.9,60)
17	0.01	49 ^{a,b,c} (3.6,2)	54 ^a (3.4,7)	47 ^c (1.0,53)	51 ^{a,b} (0.9,51)
19	0.34			44 (2.2,12)	41 (0.8,9)
22	0.80			46 (1.2,34)	45 (2.2,14)
23	0.62		48 (6.4,2)	48 (0.8,43)	46 (3.7,7)
25	0.74		43 (0.9,2)	41 (1.9,4)	43 (2.1,7)
27	0.69			41 (5.1,4)	40 (1.1,11)

discharge during the first growing season for those segments where the first growth increment differed among year classes.

Sicklefin chub

The first growth increment of sicklefin chubs differed significantly among year classes in segment 5, but not in segments 8, 9, 10, 25, and 27 (Table 8). There was no significant relationship between the first growth increment and median discharge in segment 5 ($r^2 = 0.69$, $P = 0.17$). The second growth increment of sicklefin chubs differed significantly among year classes in segments 5, 8, and 10 (Table 9), but was not significantly related to median discharge (r^2 -values 0.01 - 0.59, P -values 0.23 - 0.87) in these segments.

Freshwater drum

Lee's phenomenon was evident in mean back-calculated lengths by year class. To eliminate bias associated with back-calculation errors, otolith-growth increments rather than back-calculated length increments were used to quantify growth of freshwater drum. The first otolith-growth increment of freshwater drum differed significantly among year classes in segments 5, 15, and 25 (Table 10). The first growth increment of freshwater drum was not significantly related to median discharge in segments 5 ($r^2 = 0.47$, $P = 0.13$) or segment 15 ($r^2 = 0.82$, $P = 0.28$). In segment 25, the first growth increment of freshwater drum was significantly related to median discharge (Figure 11). A quadratic model indicated growth increased from low discharge (1,060 m³/s) to a peak at intermediate discharges (2,397-2,642 m³/s), then declined at higher discharges (3,792 m³/s).

Table 8.-Mean first-year growth increments (mm; standard error and sample size in parentheses) of the 1993-1997 year classes of sicklefin chubs in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class				
		1993	1994	1995	1996	1997
5	0.0001	54 ^a (0.5,2)	40 ^b (1.3,10)	40 ^b (0.6,39)	41 ^b (0.8,25)	
8	0.31	42 (3.0,3)	44 (2.0,6)	42 (0.5,13)	44 (1.0,17)	47 (4.1,3)
9	0.50	40 (1.2,7)	40 (1.0,16)	42 (1.0,18)	41 (0.7,22)	
10	0.46	41 (2.2,2)	39 (0.5,25)	40 (1.3,8)	38 (1.4,12)	37 (0.6,2)
25	0.99			40 (1.1,7)	40 (1.8,5)	
27	0.08			34 (0.6,4)	36 (2.0,4)	44 (5.9,2)

Table 9.-Mean second-year growth increments (mm; one standard error and sample size in parentheses) of the 1993-1996 year classes of sicklefin chubs in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class			
		1993	1994	1995	1996
5	0.02	30 ^{a,b} (3.8,2)	28 ^{a,b,c} (0.9,10)	27 ^{b,c} (0.7,32)	30 ^a (0.8,25)
8	0.05	34 ^a (3.9,3)	33 ^{a,b} (2.6,6)	33 ^{a,b} (0.8,13)	30 ^b (0.8,16)
9	0.11	32 (2.5,7)	32 (1.3,16)	33 (1.5,18)	29 (0.8,22)
10	0.003	28 ^b (6.3,2)	31 ^{a,b} (0.7,25)	35 ^a (1.3,7)	28 ^b (0.8,11)
25	0.59			37 (3.3,7)	34 (2.2,3)

Table 10.-Mean first-year otolith-growth increments (mm; one standard error and sample size in parentheses) of the 1989-1997 year classes of freshwater drum in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class								
		1989	1990	1991	1992	1993	1994	1995	1996	1997
3	0.46	0.34 (0.018,13)	0.32 (0.009,31)	0.34 (0.011,25)			0.34 (0.006,36)	0.32 (0.048,4)	0.40 (0.01,2)	
5	0.001	0.29 ^c (0.014,9)	0.32 ^{b,c} (0.014,26)	0.32 ^{b,c} (0.014,19)			0.35 ^{a,b} (0.009,31)	0.39 ^a (0.029,5)	0.37 ^a (0.011,6)	
9	0.64			0.36 (0.074,2)			0.38 (0.023,7)	0.41 (0.028,5)		
15	0.008			0.51 ^{a,b} (0.036,12)		0.39 ^b (0.016,12)				0.58 ^a (0.002,2)
19	0.53			0.58 (0.064,2)				0.50 (0.011,4)	0.57 (0.045,6)	0.49 (0.050,2)
22	0.30		0.50 (0.08,2)	0.48 (0.036,5)		0.45 (0.027,7)		0.52 (0.039,5)	0.52 (0.017,12)	
23	0.15		0.52 (0.021,3)	0.57 (0.014,3)		0.46 (0.024,9)	0.54 (0.018,13)	0.51 (0.035,6)	0.54 (0.037,5)	
25	0.004			0.45 ^c (0.03,2)		0.49 ^{b,c} (0.019,16)	0.56 ^{a,b} (0.021,11)	0.58 ^{a,b} (0.02,11)	0.59 ^a (0.015,2)	0.58 ^{a,b} (0.025,5)
27	0.25			0.56 (0.03,14)	0.58 (0.017,6)	0.48 (0.024,15)	0.55 (0.035,13)	0.56 (0.028,10)	0.50 (0.04,6)	0.56 (0.024,6)

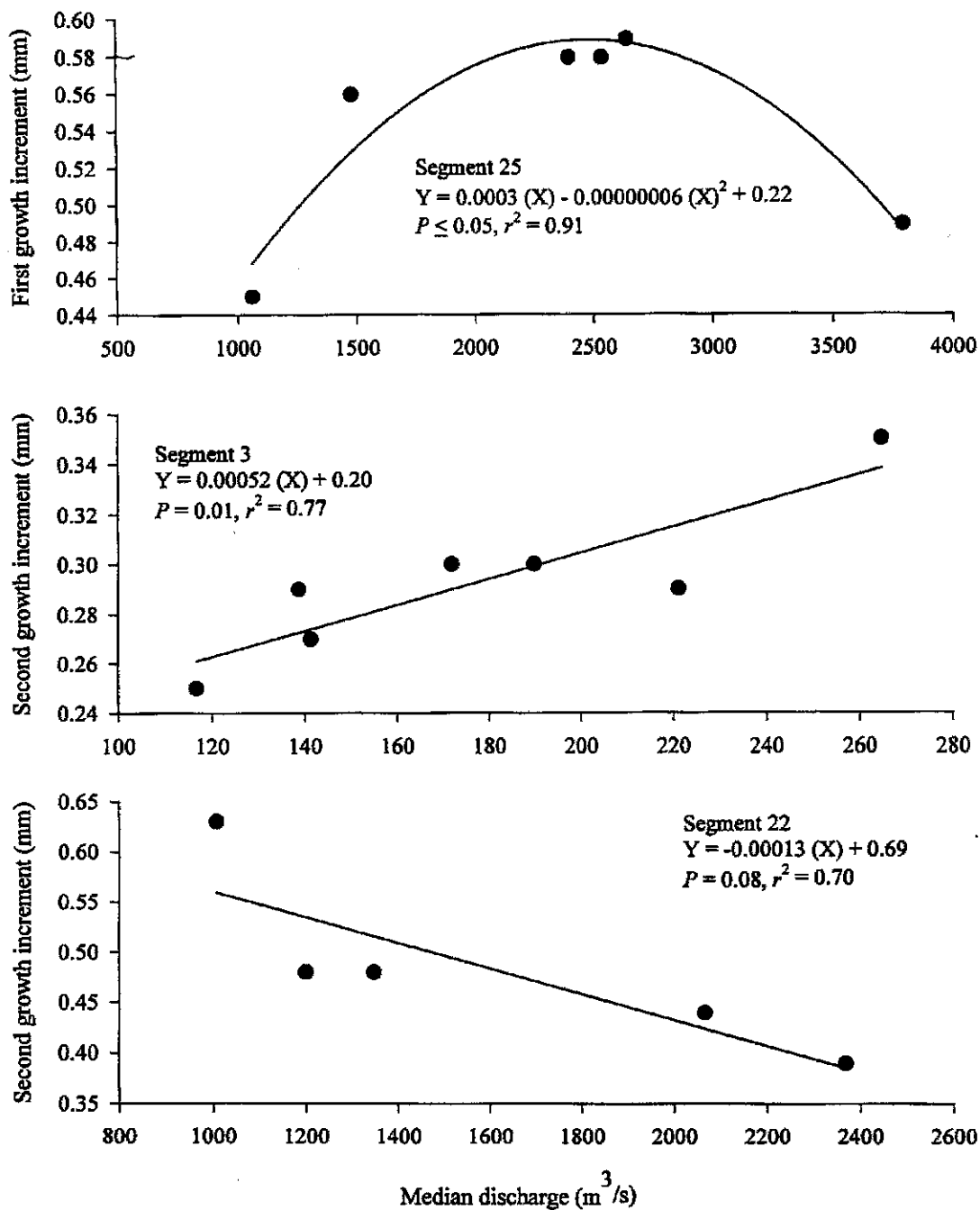


Figure 11.- Relations between mean otolith-growth increments (mm) of freshwater drum and median discharge (m³/s) during the growing season in segment 25 (top panel), segment 3 (middle panel), and segment 22 (bottom panel).

The second growth increment of freshwater drum differed significantly among year classes in segments 3, 5, and 22 (Table 11). In segment 3, there was a positive relationship between the second growth increment and median discharge (Figure 11). The second growth increment was not significantly related to median discharge in segment 5 ($r^2 = 0.28$, $P = 0.22$). In segment 22, there was an inverse trend between the second growth increment and median discharge (Figure 11).

River carpsucker

The first growth increment of river carpsuckers differed significantly among year classes in two of 16 segments (Table 12). In segment 7, the first growth increment was variable at low discharges (e.g., 150 - 250 m³/s; Figure 12), but increased substantially at a high discharge. Although there was a significant relationship between the first growth increment and discharge in segment 7 ($r^2 = 0.61$, $P = 0.04$; Figure 12), the relationship was strongly influenced by the extreme data point. There was no significant relationship between the first growth increment of river carpsuckers and median discharge in segment 10 ($r^2 = 0.01$, $P = 0.99$).

The second growth increment of river carpsuckers differed significantly among year classes in three (segments 7, 14, 23) of sixteen segments (Table 13). Similar to the first growth increment, the second growth increment in segment 7 was positively related to median discharge ($r^2 = 0.89$, $P = 0.001$; Figure 12); however, one extreme discharge strongly influenced the relationship. There was no significant relationship between the second growth increment and median discharge in segment 14 ($r^2 = 0.14$, $P = 0.62$). In segment 23, the second growth increment exhibited a curvilinear trend with median

Table 11.-Mean second-year otolith-growth increments (mm; one standard error and sample size in parentheses) of the 1988-1996 year classes of freshwater drum in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class								
		1988	1989	1990	1991	1992	1993	1994	1995	1996
3	0.0001	0.29 ^{bc} (0.013,14)	0.27 ^{bc} (0.014,13)	0.30 ^b (0.008,31)	0.25 ^c (0.006,25)			0.29 ^{bc} (0.008,36)	0.30 ^b (0.009,4)	0.35 ^a (0.008,2)
5	0.0001	0.30 ^{bcd} (0.011,13)	0.32 ^{ab} (0.012,9)	0.32 ^{abc} (0.012,26)	0.26 ^d (0.009,19)			0.29 ^{cd} (0.007,31)	0.29 ^{bcd} (0.012,5)	0.35 ^a (0.018,6)
9	0.56				0.30 (0.042,2)			0.26 (0.02,7)	0.26 (0.020,5)	
10	0.39	0.31 (0.016,2)						0.27 (0.018,6)		
15	0.99	0.44 (0.022,4)			0.44 (0.019,12)		0.44 (0.012,12)			
19	0.33	0.47 (0.007,4)			0.47 (0.043,2)				0.42 (0.009,3)	0.44 (0.039,2)
22	0.016			0.63 ^a (0.076,2)	0.48 ^b (0.036,5)		0.48 ^b (0.027,7)		0.44 ^b (0.01,4)	0.39 ^b (0.03,3)
23	0.45			0.43 (0.043,3)	0.38 (0.032,3)		0.46 (0.024,9)	0.46 (0.019,13)	0.43 (0.049,4)	
25	0.53				0.41 (0.046,2)		0.42 (0.015,16)	0.44 (0.014,11)	0.39 (0.023,6)	
27	0.31	0.47 (0.044,3)			0.49 (0.024,14)	0.54 (0.031,6)	0.48 (0.018,15)	0.47 (0.022,13)	0.43 (0.023,9)	0.47 (0.004,2)

Table 12.-Mean first-year growth increments (mm; one standard error and sample size in parentheses) of the 1989-1997 year classes of river carpsuckers in segments of the Missouri River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class								
		1989	1990	1991	1992	1993	1994	1995	1996	1997
3	0.89		63 (7.4,5)		69 (10.6,4)	64 (12.2,3)				
5	0.23		78 (10.2,2)	73 (3.9,8)	79 (5.3,8)	93 (10.7,7)	93 (7.1,4)			
7	0.02	70 ^b (5.4,2)	69 ^b (14.1,3)	82 ^{ab} (5.7,16)	69 ^b (2.8,38)	76 ^b (2.2,52)	88 ^{ab} (7.2,11)		101 ^a (5.1,2)	
8	0.76		64 (16.8,2)	71 (2.5,4)	69 (5.7,15)	70 (4.5,20)	65 (8.1,8)	59 (6.6,5)	57 (4.3,2)	54 (4.7,4)
9	0.09	61 (6.8,3)	65 (10.4,5)	65 (4.4,14)	64 (2.6,29)	63 (2.3,31)	64 (2.9,35)	81 (9.0,8)	58 (3.3,14)	55 (5.2,10)
10	0.02				64 ^b (1.8,2)	104 ^a (20.3,3)			59 ^b (1.4,6)	
12	0.79	62 (7.7,7)	74 (6.5,7)	70 (6.6,9)	64 (7.5,8)	64 (14.4,3)				
14	0.13	76 (5.6,7)	65 (5.8,10)	68 (5.1,14)	73 (3.4,24)	70 (3.7,23)	64 (4.3,17)	60 (3.1,22)	57 (6.7,5)	56 (4.7,3)
15	0.13	74 (10.1,7)	66 (5.3,9)	73 (3.6,34)	73 (2.1,92)	77 (3.0,60)	74 (6.7,8)	61 (1.5,9)	60 (4.3,4)	56 (5.7,7)
17	0.23			65 (3.0,9)	86 (7.1,10)	71 (5.1,18)	81 (8.1,9)	73 (6.1,6)	73 (5.1,8)	

Table 12. continued.

Segment	P	Year class								
		1989	1990	1991	1992	1993	1994	1995	1996	1997
19	0.25		74 (10.8,2)	75 (12.7,3)	115 (27.9,2)	86 (12.6,8)	77 (11.0,8)	74 (4.4,15)	70 (4.3,19)	
21	0.56				79 (12.9,2)	98 (21.4,3)				
22	0.08		55 (10.6,2)	61 (10.4,2)	76 (5.0,18)	69 (6.2,9)	78 (3.4,18)	70 (3.0,18)	85 (5.3,17)	
23	0.32			72 (7.4,9)	81 (7.1,13)	93 (6.4,12)	84 (0.9,2)	82 (20.0,2)	71 (4.4,5)	
25	0.55				85 (12.4,8)	96 (10.4,9)	86 (6.9,14)	79 (7.4,7)	70 (9.1,3)	62 (19.6,2)
27	0.79				81 (5.2,19)	86 (7.1,11)	85 (5.0,13)	77 (7.8,9)	91 (10.5,5)	

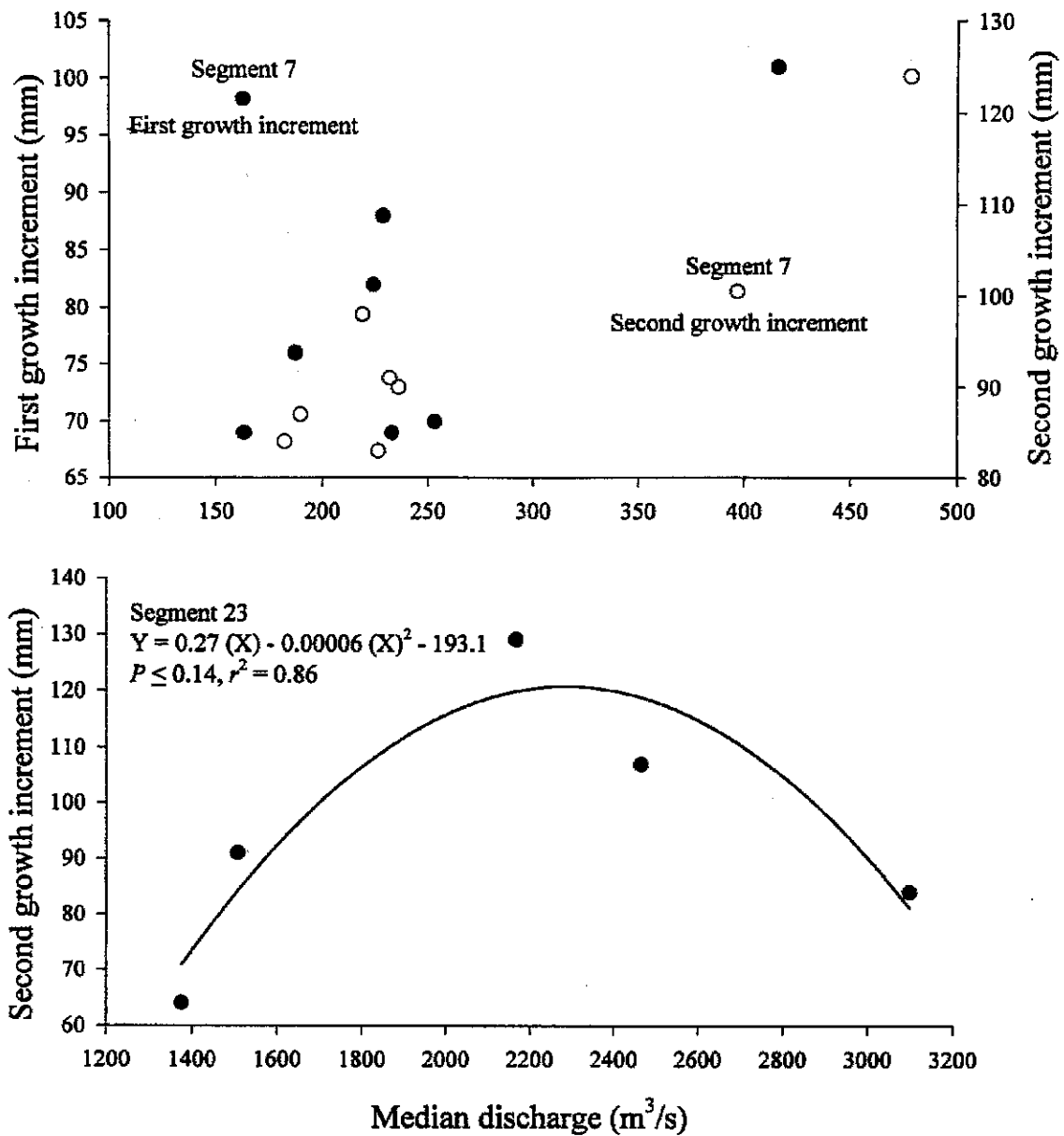


Figure 12.-Relations between mean back-calculated growth increments (mm) of river carpsuckers and median discharge (m³/s) during the growing season in segment 7 (top panel) and segment 23 (bottom panel).

Table 13.-Mean second-year growth increments (mm; one standard error and sample size in parentheses) of the 1989-1996 year classes of river carpsuckers in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different (*P* > 0.05).

Segment	<i>P</i>	Year class							
		1989	1990	1991	1992	1993	1994	1995	1996
3	0.25		89 (2.3,5)		97 (7.8,4)	81 (7.7,3)			
5	0.98		89 (5.5,2)	95 (5.7,8)	98 (8.0,8)	94 (6.9,7)	93 (15.9,4)		
7	0.04	91 ^b (10.1,2)	83 ^b (4.9,3)	84 ^b (4.0,16)	87 ^b (2.6,38)	90 ^b (2.7,52)	98 ^b (5.1,11)		124 ^a (10.0,2)
8	0.21		101 (7.2,2)	80 (9.4,4)	80 (4.6,15)	93 (3.1,20)	81 (4.9,8)	83 (11.1,4)	83 (7.9,2)
9	0.65	72 (3.3,3)	89 (12.6,5)	82 (7.4,14)	83 (4.0,29)	89 (4.1,31)	82 (2.9,35)	94 (7.5,7)	91 (8.6,6)
10	0.84				96 (7.2,2)	99 (12.3,3)			
12	0.22	92 (12.8,7)	81 (6.6,7)	84 (6.0,9)	106 (8.4,8)	101 (4.8,3)			
14	0.004	71 ^{b,c} (8.7,7)	74 ^{b,c} (7.2,10)	67 ^{b,c} (4.4,14)	81 ^{a,b} (4.5,24)	80 ^{a,b} (4.2,23)	75 ^{b,c} (5.9,17)	99 ^a (8.2,20)	55 ^c (1.9,4)
15	0.22	70 (5.8,7)	72 (3.4,9)	84 (3.2,34)	87 (2.6,92)	83 (3.5,60)	82 (6.4,8)	75 (6.2,9)	
17	0.93			84 (3.9,9)	88 (6.8,10)	82 (5.5,18)	85 (11.3,9)	76 (10.8,6)	91 (5.8,2)

Table 13.continued.

Segment	P	Year class							
		1989	1990	1991	1992	1993	1994	1995	1996
19	0.20		82 (2.0,2)	70 (3.1,3)	63 (9.0,2)	76 (7.9,8)	98 (8.4,8)	87 (6.1,8)	95 (17.2,2)
21	0.18				90 (0.3,2)	67 (10.1,3)			
22	0.43		79 (12.6,2)	69 (5.5,2)	83 (4.7,18)	87 (11.8,9)	88 (5.9,18)	88 (6.0,18)	124 (21.0,2)
23	0.008			64 ^c (6.7,9)	84 ^{b,c} (8.0,13)	92 ^{b,c} (7.1,12)	129 ^a (3.5,2)		107 ^{a,b} (5.6,3)
25	0.74				81 (7.3,8)	87 (5.6,9)	84 (6.5,14)	93 (8.2,7)	
27	0.91				85 (6.3,19)	92 (7.2,11)	85 (6.4,13)	82 (4.3,9)	89 (13.8,5)

discharge (Figure 12). A quadratic model suggested growth was small at low discharges ($1,375 \text{ m}^3/\text{s}$), peaked at intermediate discharges ($2,166 \text{ m}^3/\text{s}$), then declined at higher discharges ($3,099 \text{ m}^3/\text{s}$).

Sauger

The first growth increment of sauger differed significantly among year classes in segments 9, 10, 14, 15, 17, and 23 (Table 14). The first growth increment of sauger in segment 9 was not significantly related to median discharge ($r^2 = 0.17$, $P = 0.42$). There was a marginally significant, inverse relationship between the first growth increment and median discharge in segment 10 (Figure 13). In segment 15, there was no significant relationship between the first growth increment and median discharge ($r^2 = 0.38$, $P = 0.27$). There was an inverse trend ($r^2 = 0.71$, $P = 0.07$) between growth of sauger and median discharge in segment 17 (Figure 13). Relationships between sauger growth and discharge in segment 14 were not examined because discharge data for one of three years (1993) was not obtained.

The second growth increment of sauger differed significantly among year classes in two of ten segments (Table 15). There was a positive relationship between the second growth increment of sauger in segment 3 and median discharge (Figure 13). In segment 8, sauger growth was not significantly related to median discharge ($r^2 = 0.06$, $P = 0.76$).

Table 14.-Mean first-year growth increments (mm; one standard error and sample size in parentheses) of the 1990-1997 year classes of sauger in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different ($P > 0.05$).

Segment	<i>P</i>	Year class							
		1990	1991	1992	1993	1994	1995	1996	1997
3	0.94		170 (7.1,4)			176 (7.1,4)	175 (6.1,9)	179 (13.4,5)	170 (3.7,3)
5	0.47	189 (17.7,3)	196 (20,2)			175 (11.0,6)	169 (8.8,10)	161 (8.1,5)	180 (7.6,6)
7	0.32		177 (20.0,3)	149 (2.1,2)		180 (3.5,3)	178 (4.5,4)		
8	0.16		170 (10.8,3)		171 (18.3,2)	150 (4.7,5)	173 (6.4,6)		153 (9.8,4)
9	0.0001		218 ^a (7.0,6)		189 ^b (13.3,4)	184 ^{b,c} (5.5,11)	159 ^c (11.3,5)	161 ^c (3.4,7)	162 ^c (14.3,2)
10	0.03		175 ^{a,b} (7.8,3)	196 ^a (14.6,4)	165 ^b (16.6,2)	181 ^{a,b} (5.8,8)	161 ^b (6.4,7)	157 ^b (4.4,4)	159 ^b (8.7,6)
14	0.02				214 ^a (5.2,11)		196 ^{a,b} (11.4,4)	171 ^b (5.0,2)	
15	0.03				238 ^a (5.6,7)	245 ^a (22.3,2)	226 ^{a,b} (10.5,6)	198 ^b (8.7,6)	224 ^{a,b} (9.9,2)
17	0.004				231 ^b (9.5,9)	271 ^a (15.7,4)	212 ^{b,c} (11.2,7)	230 ^b (7.9,5)	193 ^c (7.6,4)

Table 14. continued.

Segment	<i>P</i>	Year class							
		1990	1991	1992	1993	1994	1995	1996	1997
19	0.11	231 (33.9,2)		229 (17.9,3)	261 (9.0,5)			222 (7.7,12)	
21	0.53			248 (29.1,2)	274 (20.6,5)				
22	0.13				249 (11.2,12)			210 (13.3,3)	
57 23	0.007				248 ^a (6.8,8)			198 ^b (1.7,2)	

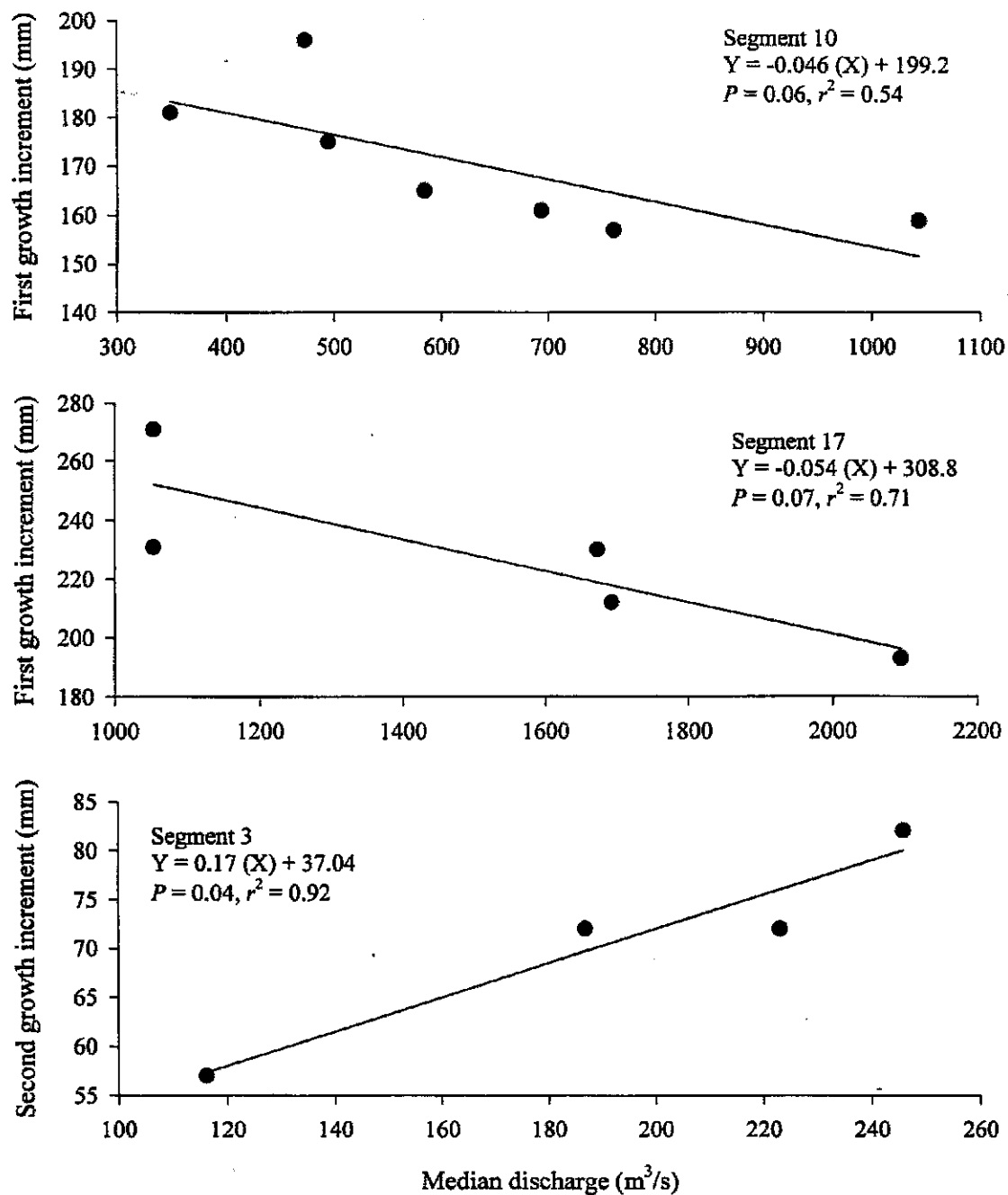


Figure 13.-Relations between mean back-calculated growth increments (mm) of sauger and median discharge (m³/s) during the growing season in segment 10 (top panel), segment 17 (middle panel), and segment 3 (bottom panel).

Table 15.-Mean second-year growth increments (mm; one standard error and sample size in parentheses) of the 1990-1996 year classes of sauger in segments of the Missouri River and Yellowstone River. Probability values (*P*) are results from a one-way ANOVA for each segment. Means with the same letter (across years) are not significantly different ($P > 0.05$).

Segment	<i>P</i>	Year class						
		1990	1991	1992	1993	1994	1995	1996
3	0.02		57 ^b (8.2,4)			72 ^a (3.3,4)	72 ^a (2.5,9)	82 ^a (4.0,4)
5	0.84	71 (18.2,3)	85 (8.9,2)			73 (6.8,6)	78 (4.2,10)	81 (8.8,2)
7	0.06		90 (4.9,3)	73 (1.2,2)		64 (5.6,3)	78 (6.2,4)	
8	0.007		60 ^b (6.1,3)		108 ^a (16.2,2)	74 ^b (3.0,5)	62 ^b (6.3,6)	
9	0.48		75 (5.8,6)		75 (3.0,4)	70 (4.6,11)	81 (3.7,5)	79 (3.5,6)
10	0.15		70 (10.6,3)	66 (14.2,4)	86 (7.6,2)	77 (5.0,8)	61 (3.2,6)	89 (4.5,3)
14	0.92				88 (6.7,11)		87 (3.2,4)	
15	0.99				97 (6.8,7)	94 (3.1,2)	98 (6.2,6)	98 (1.5,2)
17	0.36				114 (6.3,9)	99 (5.4,4)	111 (7.1,6)	
19	0.17	93 (8.0,2)		116 (7.7,3)	102 (5.4,5)			

Discussion

Latitudinal Variation in Life History Features and Growth

The latitudinal gradient of increasing water temperature, degree-days, and duration of the growing season from north to south was associated with predictable changes in several life history parameters of fishes in the Missouri River and Yellowstone River. Maximum age exhibited strong positive or curvilinear relationships with latitude for all species (except freshwater drum) which is consistent with findings from other studies across broad latitudinal gradients (Colby and Nepszy 1981; Mann et al. 1984; Beverton 1987). Whereas maximum age of river carpsucker and sauger was linearly related to latitude, maximum age of emerald shiners and sicklefin chubs was constrained by their short life spans which resulted in an asymptotic maximum age - latitude relationship. Based on temperature regulation of longevity (Beverton 1987), maximum age of emerald shiners would increase from warm, low latitudes to a biological maximum age at a higher latitude. However, because the biological maximum age threshold of emerald shiners was reached in a mid-latitude segment of the Missouri River, no additional gains in maximum age occurred at higher latitudes despite cooler water temperatures. A similar pattern was found for sicklefin chubs, but maximum age further increased as water temperatures decreased along the latitudinal gradient because sicklefin chubs generally live 1-yr longer than emerald shiners. Although maximum age - latitude relationships were significant for emerald shiners, sicklefin chubs, river carpsuckers, and sauger, maximum age of freshwater drum was only weakly related to latitude.

Inverse relationships between K and latitude or positive relationships between K and water temperature for river carpsuckers and sauger are natural life-history patterns that have also been observed in other studies (Beverton 1987; Lobon-Cervia et al. 1996). Although not statistically significant, there was also evidence that K was positively related to water temperature for freshwater drum. Mechanisms underlying latitudinal gradients in K and longevity in the Missouri River are not specifically known; however, several factors related to water temperature may provide a basis for patterns observed in the Missouri River and Yellowstone River. Beverton (1987) concluded that K was a direct function of water temperature due to direct influence of water temperature on growth rate processes. Latitude and water temperature may also indirectly influence K. For example, because natural mortality increases from north to south concomitant with increasing water temperature (Beamesderfer and North 1995), latitudinal variations in K reflect plastic responses to differential mortality due the strong correlation between K and mortality (Pauly 1980; Charnov and Berrigan 1991; Wootton 1992). The finding that longevity of fishes in the Missouri River and Yellowstone River increased from south to north supports this hypothesis. These results support a broader knowledge base which indicates fish populations in southern latitudes are characterized by a relatively short life-span and rapid growth during their life span; whereas, fish populations in northern latitudes have a longer life span and slower growth.

Mean length at age was the third life history parameter exhibiting strong correlations with latitude; however, relations between length at age and latitude varied among species. For river carpsuckers, length at ages 6 - 8 increased with latitude which

likely reflects latitudinal variations in age at maturity. For example, if river carpsuckers reached sexual maturity at an earlier age or smaller length in lower, warmer latitudes which is consistent with other studies (Colby and Nepszy 1981; Beverton 1987; Rijnsdorp 1993; Lobon-Cervia et al. 1996), then more energy at older ages would be partitioned into gonadal development than somatic growth. Age at maturity is not known for high-latitude populations, but in Iowa, river carpsuckers reach sexual maturity at 4 - 5 years (Buchholz 1957; Behmer 1965). Although a pattern of increasing size with latitude was observed for river carpsuckers in this and in other studies (e.g., Bergmann's rule, Lindsey 1966; Holcik and Jedlicka 1994; Taylor and Gotelli 1994), length at age of sauger (ages 1 - 5) and freshwater drum (ages 4 - 6, and probably 7 - 9) was inversely correlated with latitude. These results do not support predictions of Bergmann's rule. Lobon-Cervia et al. (1996) similarly observed length at age of dace *Leuciscus leuciscus* was smaller in cooler than warmer locations. Maturity age for sauger varies from 2 - 8 years, and increases from south to north (Carufel 1963; Vasey 1967; Carlander 1997). Freshwater drum in low- and mid-latitudes mature at 2 - 4 yr (Wrenn 1968; Goeman 1983; Bur 1984), and it is likely that age at maturity is greater in northern latitudes. Thus, higher growth at older ages despite earlier maturation may be maintained by sauger and freshwater drum in lower latitudes due to higher aquatic production and food resources.

Latitudinal regulation of fish life history parameters in the Missouri River and Yellowstone River should be viewed with caution because all segments in the lower latitudes (i.e., segments 17 - 27) were located in the channelized portion of the Missouri River. Channelization and other anthropogenic modification may alter life history

parameters independent of latitudinal effects. For example, Przybylski (1996) found longevity of roach *Rutilus rutilus* increased from north to south among river segments differentially affected by pollution and channelization; however, this pattern was not maintained in pike *Esox lucius* or chub *Leuciscus cephalus*. Similarly, Przybylski (1996) found K and lifespan of roach were inversely related, but in this case the relationship was driven by anthropogenic river modifications rather than latitude. Torralva et al. (1997) found *Barbus sclateri* were longer - lived in a non-regulated than regulated river section, and reached maturity at younger ages and lengths in a non - regulated than regulated river section. Although the extent of anthropogenic modifications varies substantially among river segments and latitudes in the Missouri River, consistent latitudinal trends between this study and other studies suggest latitudinal variation in water temperature exerts a stronger influence on life history parameters than variations in in-stream habitat.

Relationships between growth increments during the first growing season and latitude varied greatly among species. In contrast, growth rates of emerald shiners, sicklefin chub, freshwater drum, and river carpsucker during the first growing season were strongly and positively correlated with latitude. Similar growth rate increases for these species suggest a common interspecific growth response to latitude. Positive relationships between growth rate and latitude or inverse relationships between growth rate and water temperature (the inverse of latitude) among latitudinally distant populations have been observed in several studies (Conover 1990; Conover and Present 1990; Lobon -Cervia et al. 1996; Conover et al. 1997; Power and McKinley 1997). Rapid growth rates during the first growing season may enable fishes in northern latitudes to

reach suitable lengths and acquire energy reserves, thereby reduce the likelihood of size-selective overwinter mortality (Conover 1990) that has been demonstrated in fishes (Post and Evans 1989; Johnson and Evans 1990; Hurst and Conover 1998; Schlosser 1998). Because the likelihood of size-selective overwinter mortality due to energy depletion decreases from north to south (Post and Evans 1989), rapid growth of fishes in southern latitudes is not a prerequisite to survival, at least from an energy - accumulation standpoint. The four species (emerald shiner, sicklefin chub, freshwater drum, and river carpsucker) exhibiting positive relations between growth rate and latitude are taxa exhibiting relatively small first growth increments - a phenotypic characteristic resulting from delayed spawning (late spring - early summer) and short duration of the growing season. If there is a minimum size threshold for surviving winter, then growth rates should increase from south to north to achieve that threshold. The minimum back-calculated length at age-1 of species examined in this study was 29 mm (emerald shiners), 29 (sicklefin chubs), 65 mm (freshwater drum), and 32 mm (river carpsucker). Minimum size thresholds for survival through winter have been found in other studies (Henderson et al. 1988; Schlosser 1998). In contrast, sauger spawn earlier, have a longer growing season, and are consequently larger at the beginning of winter. The risk of overwinter mortality related to energy depletion is likely reduced in sauger at all latitudes due to their greater lengths prior to winter. This conclusion is supported by Madenjian et al. (1996) who found no evidence of over winter mortality in the congeneric walleye *Stizostedion vitreum* where individuals as small as 110 mm survived winter. In this study, the minimum length of sauger was 127 mm.

Countergradient variation in growth rates does not require that growth increments correlate positively with latitude. Growth increments increased, decreased or exhibited a curvilinear or no relationship with latitude which is consistent with other studies (Conover 1990; Conover and Present 1990). For example, Conover and Present (1990) found that although growth rates were greater for Atlantic silversides *Menidia menidia* from high-latitude populations, body size at the end of the first growing season initially increased with latitude, then stabilized or declined at higher latitudes. These results suggest faster growth rates characteristic of northern populations may not fully compensate for the reduced duration of the growing season.

Results from controlled studies where fishes collected from different latitudes were raised in common environments have revealed a genetic basis to growth rate differences among populations (Conover and Present 1990; Nicieza et al. 1994; Conover et al. 1997). In contrast, Oliveira (1999) did not find latitudinal compensation in growth rate of American eels *Anguilla rostrata*. He suggested that the panmictic spawning behavior of eels removes genetic influences, and prevents selection from acting on the countergradient pattern of growth rate. In the Missouri River, it is not known whether latitudinal variations in growth rates from north to south reflect discrete genetic differences among populations or reflect phenotypic plasticity to varying thermal gradients. Only under controlled studies can the genetic or plasticity basis of growth rate be determined.

Physiological mechanisms related to latitude and water temperature provide a second likely explanation for the strong correlations between growth rates of fish and

latitude. Nicieza et al. (1994) provided a proximate-level mechanism for the countergradient growth pattern. They found digestive performance and efficiency of Atlantic salmon *Salmo salar* was greater for high than low latitude populations when both populations were raised under common environments. This finding may also provide an explanation for the countergradient growth paradox (e.g., Conover et al. 1997): if rapid growth during the first growing season enhances fitness, then why are growth rates of fishes in southern latitudes sub-optimal? If digestive efficiency is genetically regulated and relatively static in populations from southern warmer latitudes (Nicieza et al. 1994), then growth may be constrained in southern populations. Results from Nicieza et al. (1994) may similarly provide a mechanism to explain why the countergradient growth pattern was not restricted to growth during the first growing season. Growth rates of river carpsuckers during the second growing season were positively related to latitude. Power and McKinley (1997) also observed that growth rates of age-15 lake sturgeon *Acipenser fulvescens* were positively correlated with latitude.

Results from OGF analyses indicated patterns in growth rate for emerald shiners and sauger were not an artifact of a latitudinal gradient in water temperature supporting optimal growth. On the contrary, growth rate in emerald shiners was higher at low OGF (high latitudes). This result lends additional support to the countergradient growth hypothesis (Conover 1990; Conover and Present 1990; Conover et al. 1997). Lack of a correlation between growth rate and OGF in sauger suggests factors not directly related to water temperature influence growth rate in this species. Similar OGF analyses for sicklefin chub, river carpsucker, and freshwater drum were not conducted due to the lack

of growth - temperature models. However, given that spawning temperatures and growing season duration for these species are similar to those for emerald shiners, I would expect similar results for sicklefin chub, river carpsucker, and freshwater drum.

Relations between growth and water velocity used by fishes during the first growing season suggest water velocity, in addition to latitude, is another factor influencing growth of fishes in the Missouri River. Interpretation of analyses involving velocity rests on the assumption that mean column velocity adequately quantifies velocity used by fishes in this study. Positive relations between growth and velocity use in emerald shiner, sicklefin chubs, freshwater drum, and sauger are intriguing because use of higher velocities by fishes during the first growing season would impose greater metabolic demands, and likely reduce energy available for somatic growth. One mechanism to offset increased energetic demands imposed by high velocities is to modify body morphology by increasing body length (e.g., become more streamlined; Gordon et al. 1992). Several studies have demonstrated intraspecific morphological plasticity in fishes (e.g., Beacham et al. 1988, 1989; Keenlyne et al. 1994; Holopainen et al. 1997). Phenotypic plasticity is a labile trait (Scheiner 1993) that could account for changes in body length of emerald shiners and freshwater drum across the different river segments. Greater first growth increments at higher velocities may reflect morphological adaptation, in that increased length due to streamlining would be reflected in greater lengths. Whereas positive relations between growth rate and velocity in freshwater drum and sauger are likely related to streamlining, the positive relation between growth rate and velocity for sicklefin chubs reflects latitudinal increases in growth rate because latitude

and velocity were positively correlated. On the contrary, growth rate and velocity use were inversely correlated for river carpsucker suggesting higher velocities constrained growth in this species.

Strong correlations with latitude, and to a lesser extent water velocity, do not preclude the possibility that other factors influence growth rates of fishes in the Missouri River and Yellowstone River. As predicted by generalized models of riverine ecosystems, water temperature, discharge and productivity change from upstream to downstream (e.g., Vannote et al. 1980). Similarly, river segments examined in this study vary considerably in water temperature, discharge, instream habitat, and probably food resources. Differences in food availability have been linked to interpopulation growth rates (Chen and Harvey 1995), and may provide a basis for growth rate differences in this study. Emerald shiners less than 35 mm feed predominantly on algae, but switch to zooplankton at larger lengths (Fuchs 1967). River carpsuckers feed on periphyton and associated organisms (Brezner 1958). Sicklefin chubs (Weldon 1993) and age-0 freshwater drum greater than 20 mm (Swedberg and Walburg 1970) are benthic insectivores. Given the consistent interspecific linear increase in growth rates of these species along the Missouri River latitudinal gradient, food availability should similarly follow a downstream to upstream trend if food limitations constrain growth rates. Although quantitative information on food resources and aquatic productivity is lacking for the majority of the river segments (Hesse et al. 1982a), available information suggests that food production may increase, rather than decrease, from upstream to downstream. For example, Martin et al. (1980) found turbidity, gross and net primary productivity,

phytoplankton standing crop, and chlorophyll *a* concentrations increased from upstream to downstream reservoirs on the Missouri River. Benson and Colwell (1968) similarly found diatom densities were greater in the lower Missouri River at Yankton, South Dakota (8 km downstream from Gavins Point Dam) than at the headwaters of Lake Sakakawea in North Dakota. In the lower river, Morris et al. (1968) found standing crops of benthos were similar between unchannelized and channelized reaches. Novotny (1978) found densities of drifting macroinvertebrates increased from upstream study areas (located in segments 14, and 15) to a downstream study area in the channelized river, and concluded higher densities were attributed to high macroinvertebrate production that occurs along the riprap shorelines of the channelized river. Hesse et al. (1982a) similarly surmised the abundance of limestone riprap has enhanced aquatic production in the channelized Missouri River. An increase in the abundance of zooplankton from downstream to upstream as a result of an increasing number of reservoirs from downstream to upstream may offer emerald shiners in the mid- and high latitudes a food advantage; however, this benefit is likely minimal because emerald shiners during much of the growing season (e.g., < 35 mm) feed on algae (Fuchs 1967). These results suggest that the low growth rates of emerald shiners, sicklefin chubs, freshwater drum, and river carpsuckers in the lower river were not a result of food or nutrient limitation as speculated by Arendt (1997). On the contrary, evidence suggests that growth rates increase from south to north against a gradient of decreasing food availability.

There is strong evidence to suggest that the inverse relationship between growth rates of sauger and latitude is related to prey availability. Sauger greater than 70 mm are

piscivores (Nelson 1968; Hesse et al. 1982b), and feed predominantly on emerald shiners and gizzard shad in large rivers (Wahl and Nielsen 1985). Gizzard shad are restricted to the lower segments of the Missouri River (i.e., segments 14-27); whereas, emerald shiners are ubiquitous in the basin. Wahl and Nielsen (1985) found sauger fed on emerald shiners during summer, but switched to gizzard shad during fall as water temperature declined. They suggested that rapid growth rates during fall were attributed to the switch to gizzard shad prey whose vulnerability to predation increased relative to emerald shiners at cooler water temperatures. Based on these findings, the absence of gizzard shad in high-latitude river segments may provide a basis for declining growth and growth rates of sauger from south to north.

Lack of information on growth increments and growth rates of fishes in the Missouri River prior to river modifications precludes determining the extent to which river modifications have affected growth. Morris (1965) reported length at age data for river carpsuckers collected in the Missouri River between Sioux City, Iowa and Omaha, Nebraska (e.g., segment 17). This study was conducted during the early years (1961-1962) of channelization when permeable pile dikes were being replaced with impermeable rock dikes (Galat et al. 1996), but following closure of Gavins Point Dam in 1955. Lengths of river carpsuckers at age-1 (mean = 74 mm) and age-2 (mean = 157 mm) reported by Morris (1965) are similar to those found in this study for segment 17 (age-1, mean = 85 mm; age-2, mean = 158 mm). Similarity in length at age data between studies suggests cumulative effects of channelization have not negatively affected growth of river carpsuckers in segment 17 of the channelized Missouri River.

Segment-level Growth Response to Discharge

Species varied in their growth response to discharge among segments. Relations between growth increments and discharge for emerald shiners and sicklefin chub were hindered by low sample size due to their short life span and short duration of this study. Nonetheless, there was little evidence to suggest that growth of emerald shiners and sicklefin chub was influenced by discharge in any Missouri River segment. In contrast, there was strong evidence that growth of freshwater drum, river carpsucker, and sauger in some segments was related to discharge. Gutreuter et al. (1999) hypothesized that growth of typical floodplain species (e.g., largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*) should be most sensitive to interannual variations in discharge; whereas, growth of riverine species (e.g., white bass *Morone chrysops*) not typically associated with the floodplain should be relatively insensitive to interannual variations in discharge. Results from this study contradict the hypothesis of Gutreuter et al. (1999), and suggest that growth of freshwater drum, river carpsucker, and sauger - species not typically associated with the floodplain - is influenced by interannual variations in discharge during the growing season.

Mechanisms underlying differential growth responses to discharge among segments for freshwater drum, river carpsucker, and sauger are unknown, but likely include segment - level differences in the magnitude of discharge, and its subsequent affect on food production and habitat suitability. Positive relations between discharge and growth of freshwater drum and sauger in segment 3 are patterns consistent with predictions from natural floodplain river ecosystems where increases in discharge

increase wetted surface area, and subsequently enhance aquatic productivity (e.g., the flood pulse; Welcomme 1979; Bayley 1988; Junk et al. 1989; Bayley 1991). The quadratic growth response to discharge for river carpsuckers in segment 23 and freshwater drum in segment 25 similarly suggest growth increases with increasing discharge; however, extreme discharges negatively influence growth. The decline in growth for both species occurred in 1993 when record floods during summer occurred in the lower Missouri River basin (i.e., segment 23 median = 3,099 m³/s; segment 25 median = 3,793 m³/s). These results suggest benefits of increased productivity associated with flood conditions were partially offset in segments 23 and 25 by other factors such as the reduced availability of low-velocity habitat. For example, the channel in segments 23 and 25 is constrained by riprap which may increase main channel velocities during flood conditions.

Whereas growth of fishes was positively related to discharge in segments 3, 23, and 25 except during periods of extreme discharge, growth of freshwater drum in segment 22, and sauger in segments 10 and 17 was negatively related to discharge. Lyons and Welke (1996) similarly provided evidence that growth of sauger in the Wisconsin River was inversely related to water levels (a correlate of discharge), but did not find a similar response in Mississippi River sauger. Rutherford et al. (1995) also found growth of freshwater drum was negatively correlated with discharge. Rutherford et al. (1995) concluded that higher water clarity at lower discharges increased food production which resulted in better growth during low discharge years. Discharge-related variations in turbidity and its subsequent effect on aquatic productivity may provide an explanation for

the negative growth response to discharge in segments 10, 17, and 22 and the positive growth response to discharge in segment 3. Segment 3 generally has lower turbidity than other Missouri River segments exclusive of those immediately downstream from dams (Dieterman et al. 1996, Young et al. 1997). Due to its upstream location in the watershed and scarcity of tributaries (Braaten and Guy 1995), significant increases in turbidity in segment 3 may not occur as discharge increases. As a consequence, aquatic production and fish growth in segments 3 and 7 may increase with increasing discharge as wetted surface area of the channel increases. In contrast, turbidity is higher in segment 10 (due to inputs from the Yellowstone River), and segments 17 and 22 (Dieterman et al. 1996; Young et al. 1997). Increases in discharge in these segments may reduce aquatic production and negatively impact growth.

River carpsucker in segment 7 of the Missouri River exhibited a threshold response to discharge where growth increments were small through a range of low to moderate discharges, but large at high discharges. Interactions between discharge and channel morphology, and the subsequent influence of these interactions on aquatic production provide a likely explanation for the differential growth response. Because segment 7 is located downstream from Ft. Peck Dam, channel degradation has isolated backwaters and other off-channel areas from the main channel except during periods of high discharge (M. Ruggles, Montana Department of Fish, Wildlife and Parks, personal communication). Greater growth in 1996 (first growth increment) and 1997 (second growth increment) likely reflects enhanced aquatic productivity and food availability that resulted from inundation of backwaters and other off-channel areas at higher discharges.

Results from this study suggest latitude and its water temperature correlates (e.g., degree-days, number of days in the growing season) influence growth and life history characteristics of emerald shiner, sicklefin chub, freshwater drum, river carpsucker, and sauger across the broad spatial gradient of the Missouri River. Although this conclusion is consistent with previous investigations, additional studies are needed to identify mechanisms underlying the latitudinal patterns. At smaller spatial scales, inter-annual variation in discharge during the growing season influences growth of some, though not all species. However, discharge mediates differential growth responses among species and river segments.

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Chapter 2

Recruitment dynamics of freshwater drum in the lower channelized Missouri River

Introduction

Flowing water is a fundamental feature of streams and rivers which influences numerous physical and biological processes. Lateral flow which typically occurs during flood conditions is a mechanism driving land-water nutrient exchange pathways, and aquatic production in many lotic ecosystems (Welcomme 1979; Junk et al. 1989; Bayley 1991; Welcomme 1995). In contrast to lateral flow, unidirectional (longitudinal) flow which occurs during base flow, floods and nonflood conditions is the primary mechanism linking physical and biological processes along the longitudinal gradient. As a consequence of unidirectional flow, landscape disturbances or hydrologic alterations in the upstream portions of the watershed can ultimately affect aquatic communities and habitat structure in downstream areas. Identification of upstream to downstream linkages has provided the foundation for conceptual models of lotic ecosystem processes (Vannote et al. 1980; Wiley et al. 1990).

Eggs and larvae of many fish species are transported via water currents from upstream spawning areas to downstream settling areas (Cada and Hergenrader 1980; Muth and Schmulbach 1984; Mitro and Parrish 1997; Robinson et al. 1998). Thus, unidirectional flow can influence spatial variations in fish recruitment. Analogous water current-larval transport dynamics exist in marine systems where benthic colonizers at a location originate from up-current spawning areas (Victor 1986; Doherty 1991; McNeil et

al. 1992; Danilowicz 1997). Thus, there is the high probability that patterns of juvenile recruitment in down-current areas of rivers are dependent upon up-current spawning success, larval delivery and survival, and colonization success in down-current areas. In the marine environment, spatial and temporal variations in larval supply in conjunction with water current transport dynamics have been used to explain variability in fish recruitment. For example, recruitment-limitation models (Victor 1986; Doherty 1991; Doherty and Fowler 1994) infer that recruitment is proportional to the initial supply of larval settlers, and that mortality of juveniles is density-independent when initial densities are below carrying capacity (Victor 1986). However, several studies have also demonstrated that density-dependent mortality is an additional process regulating recruitment (Forrester 1990, 1995; Caselle 1999; Schmitt and Holbrook 1999a, 1999b).

In freshwater ecosystems, variation in the abundance of river-spawned eggs and larvae are useful in predicting temporal variations in recruitment for slack-water environments at the river terminus (e.g., lakes and reservoirs; Bulak et al. 1997; Mitro and Parrish 1997; Mion et al. 1998; Chick and Van Den Avyle 1999). In these demographically closed populations, the terminal lentic environment provides the settling area for larvae; however, in demographically open systems, such as free-flowing rivers, local recruitment is uncoupled from local reproduction by a dispersive larval stage (Caley et al. 1996; Danilowicz 1997). Free-drifting larvae in open systems may add to the existing ichthyoplankton population throughout the longitudinal gradient. Similarly, the ichthyoplankton population may be differentially affected by mortality along the

longitudinal gradient due to differences in larval density and size (Crecco and Savoy 1987a, 1987b; Houde 1997).

If spawning occurs throughout the longitudinal gradient (e.g., multiple larval sources), and spawning success is similar at all sources (e.g., egg to larval survival is equal), then similar larval densities at all downstream sites may result. In this instance, juvenile abundance would be similar among downstream sites given a strong correlation between larval and juvenile densities. In contrast, if spawning does not occur continuously throughout the longitudinal gradient, juvenile distributions in downstream areas will be patchy, and reflect spatial variations in larval supply, and differential larval settlement and mortality rates.

Larval numbers may positively correlate with juvenile abundance, but abundance of juveniles may not be an adequate predictor of year-class strength. Winter is a second critical period in the life history of fishes (Shuter et al. 1980; Schlosser and Angermeier 1990; Hurst and Conover 1998; Schlosser 1998). Field and laboratory studies (Oliver et al. 1979; Toney and Coble 1979; Conover and Ross 1982; Henderson et al. 1988; Post and Evans 1989; Johnson and Evans 1990; Miranda and Hubbard 1994; Kirjansniemi and Valtonen 1997; Hurst and Conover 1998; Post et al. 1998; Schlosser 1998; Schultz et al. 1998) have demonstrated that overwinter mortality can reduce juvenile populations, with smaller individuals generally experiencing greater overwinter mortality than larger individuals. However, this pattern is not consistent among fish species in all aquatic environments (Toney and Coble 1979; Madenjian et al. 1996; Hurst and Conover 1998). Abiotic factors including winter duration, and severity of winter water temperatures may

influence the magnitude of size-selective overwinter mortality (Bodensteiner and Lewis 1992; Hurst and Conover 1998).

In addition to abiotic factors, biotic factors may contribute to size-selective overwinter mortality. If feeding occurs during winter conditions, predators may alter the size structure of their prey by feeding on the smallest, most vulnerable prey in the population (Miranda and Hubbard 1994). This pattern would increase the mean length of the prey population through winter, and infer predator-induced size-selective overwinter mortality. A similar pattern of increasing mean length of the population may be observed if larger individuals are more efficient at feeding than smaller individuals, especially if food resources are in short supply. Indirectly, competition for food during the first summer of life may affect pre-winter growth and condition of fish, and enhance the potential for overwinter mortality (Schlosser 1998).

In this study, I examine sources, growth, and mortality of larval freshwater drum *Aplodinotus grunniens*, and explore interactions among larval transport and mortality, juvenile abundance, and overwinter mortality in four spatially segregated study areas of the lower channelized Missouri River. Freshwater drum is an ideal species to examine relations between larval transport, colonization success, and recruitment in open, lotic ecosystems due to its pelagic spawning habit (Swedberg and Walburg 1970) and vulnerability of eggs and larvae to transport via river currents (Swedberg and Walburg 1970; Walburg 1971; Cada and Hergenrader 1980). Results from previous ichthyoplankton studies in the lower channelized Missouri River (Kallemeyn and Novotny 1977; Tondreau 1979; Cada and Hergenrader 1980; Hergenrader et al. 1982)

have led to the hypothesis that Lewis and Clark Lake (a Missouri River mainstem impoundment) and an unchannelized reach of the Missouri River are the primary spawning sites and sources of larval freshwater drum in the Missouri River. Three hypotheses were tested to evaluate interactions between larval sources, juvenile recruitment, and overwinter mortality of freshwater drum in the lower channelized Missouri River. First, if Lewis and Clark Lake and the unchannelized reach of the Missouri River are the primary spawning areas and sources of larval freshwater drum for the channelized Missouri River, then the abundance of larval freshwater drum in the channelized river should decrease from upstream to downstream sites (prediction 1), and the larval composition at all sites should be comprised of individuals originating from the Lewis and Clark Lake and unchannelized river sources (prediction 2). Second, if juvenile recruitment is completely dependent upon larval supply, then there will be a positive, linear relationship between site-level densities of settling larval freshwater drum and catch rates of age-0 freshwater drum (prediction 3). Third, if year class strength is strongly related to survival through winter, then smaller individuals in the population will incur greater overwinter mortality than larger individuals (prediction 4), and size-selective overwinter mortality will reduce juvenile numbers (prediction 5).

Study Area

The Missouri River from Sioux City, Iowa to its confluence at the Mississippi River near St. Louis, Missouri (Figure 1) has been extensively modified by channelization activities to accommodate river navigation. Outside-bend shorelines have been

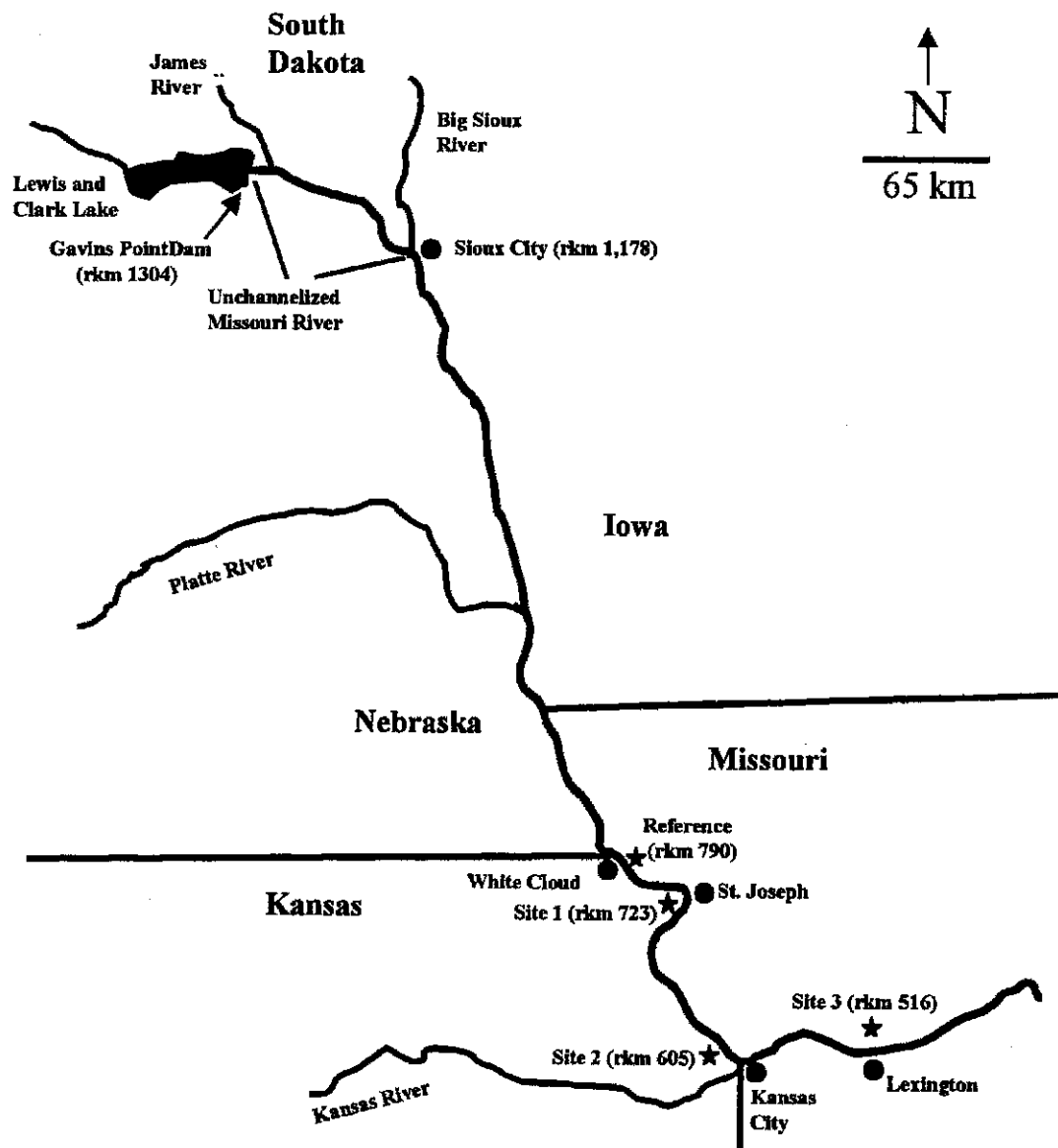


Figure 1.-Locations of study sites (reference, sites 1, 2, 3; indicated by stars) and other features in the lower Missouri River. Distance upstream from the mouth of the Missouri River is denoted by river kilometers (rkm).

constricted with riprap, and numerous wing dikes have been constructed on inside bends and other areas to concentrate flows into a single navigation channel. Off-channel areas (e.g., side channels, backwaters) and shallow sand bar habitats have been nearly eliminated throughout much of the lower river from channelization activities (Funk and Robinson 1974; Hesse et al. 1989). As a result of channelization, main channel velocities are high (Slizeski et al. 1982), and areas of low velocity are primarily restricted to tributary mouths (Dames et al. 1989; Brown and Coon 1994; Braaten and Guy 1999), pools created by wing dikes, and interstitial spaces in the riprap.

Discharge in the Missouri River is regulated by discharge releases through Gavins Point Dam. Gavins Point Dam impounds Lewis and Clark Lake (surface area 11,300 ha; Figure 1), the lower-most of six mainstem impoundments on the Missouri River. Between Gavins Point Dam and the channelized river is an unchannelized, relatively natural reach of the Missouri River. Numerous sand bars, islands, secondary channels, and off-channel embayments occur throughout this reach, but inundation of these habitats is affected by discharge releases from Gavins Point Dam (Kallemeyn and Novotny 1977; Latka et al. 1993; Mestl and Hesse 1993). Water released through Gavins Point Dam is drawn from just below the lake surface to the reservoir bottom (Walburg 1971), and is increased from April through late November or early December to facilitate navigation in the channelized river. During the non-navigation season, flows in the channelized river are at levels one-half to two-thirds of the navigation season flows (Hesse and Newcomb 1982; Latka et al. 1995). Discharge in the upper reaches of the channelized river are most strongly influenced by flow releases from Gavins Point Dam; whereas, tributary inputs

(e.g., Platte River, Kansas River) in the middle and lower reaches of the channelized river attenuate the influence of Gavins Point Dam releases.

Four study sites were established in a 274-km reach of the Missouri River (Figure 1). Sites were ordered sequentially from upstream to downstream as the reference site (White Cloud, KS), site 1 (St. Joseph, MO), site 2 (Kansas City, MO), and site 3 (Lexington, MO). Adjacent study sites were separated by 67-118 rkm, and correspond closely to river segment 21 (site 1), segment 22 (site 2), and segment 23 (site 3) referred to in Chapter 1 and outlined in Dieterman et al. (1996) and Young et al. (1997). The reference site was established to provide an initial estimate of larval numbers entering the study reach. Other sites quantified larval dynamics (e.g., growth, mortality, settling) that occurred between each successive site.

Methods

Larval Freshwater Drum

Sampling.-Larval freshwater drum were collected at 1-week intervals from mid to late May through July in 1997 and 1998 at the four study sites (Figure 1). These dates coincide with the time period when larval freshwater drum are most abundant in the drift (Harrow et al. 1975; Cada and Hergenrader 1980; Hergenrader et al. 1982) based upon the initiation of spawning at 18°C (Swedberg and Walburg 1970). In 1997, larval freshwater drum were collected at five bends in each site. Three of the original five bends sampled in 1997 were randomly selected and sampled in 1998. Bends at each site were selected as replicate sampling areas because I was primarily interested in examining

cumulative changes in larval abundance between sites. Thus, replicate bends at each site were treated as fixed sampling stations. Larval fish samples were collected near the midpoint of each bend, 20 - 40 m from the inside bend shoreline. Two or three consecutive days were required to complete sampling at all sites.

Larval freshwater drum were collected using 0.5-m-diameter bongo nets (500 μ m mesh) fitted with a General Oceanics Model 2030 velocity meter at the net opening. The bongo net apparatus (e.g., frame and two nets) was suspended with a boom from the bow of the boat. After the bongo nets were deployed, boat position was maintained by referencing a fixed point on shore. Sample duration varied between 210 - 540 s (mean = 416 s) depending on detrital loads and water velocity. Water velocities at the point of sampling varied between 0.13 - 1.28 m/s (mean = 0.71 m/s). Larval fish samples were frozen on dry ice immediately after capture.

Laboratory procedures. -Freshwater drum were distinguished from other larvae based on morphometric and meristic criteria in Auer (1982). Freshwater drum were measured to the nearest 0.1 mm (total length) using a length-calibrated image analysis system. Individuals that were damaged or broken were not measured. Following morphological developmental stages of freshwater drum (Swedberg and Walburg 1970; Fuiman 1982), individuals less than 16 mm were classified as larvae.

After length measurements and enumeration were completed for each sample, sagittal otoliths were removed from a randomly selected sample (37 - 63 individuals) of larval freshwater drum stratified by year and site. Otoliths were affixed to glass slides (sulcus side down; Zigler and Jennings 1993) using thermoplastic cement. Whole

otoliths were viewed under 100 - 400 magnification with a standard light microscope. Otoliths were ground to the nucleus using 1200 grit wet-dry sand paper, and polished with 0.3 μm -alumina paste when the nucleus or innermost rings were not clearly discernable. Grinding and polishing were needed on most individuals greater than 10 mm. Otoliths from all individuals were aged by two independent readers. Final age assignments were determined by averaging readings from both readers. Formation of daily growth rings on otoliths has not been validated for freshwater drum. However, daily increment formation has been validated in studies of other sciaenids (e.g., *Sciaenops ocellatus*; Peters and McMichael 1987). I assumed daily increment formation on sagittae for freshwater drum based on confamilial patterns of daily ring deposition rates. This assumption is supported because growth rates and the intercept of length at age models (e.g., length at hatch; see Results) were similar to values based on laboratory studies of larval freshwater drum (Swedberg and Walburg 1970).

Statistical analyses.-All statistical analyses were conducted using SAS (1990). A two-way analysis of variance (ANOVA) was used to compare densities of larval freshwater drum (number/100 m³) among weekly sampling intervals (fixed factor) and study sites (fixed factor) for each year. Separate two-way ANOVAs were used for each year because water temperatures reached the 18°C spawning threshold earlier in 1998 than 1997; therefore, the 1998 data set included sampling dates not present in the 1997 data set. To compare densities of larval freshwater drum between years, dates of peak larval densities were compared using a two-way ANOVA (year x site). Prediction 1 was tested using regression analysis where distance downstream from Gavins Point Dam was

the independent variable and site-level density of larval freshwater drum was the response variable.

Growth of larval freshwater drum (< 16 mm) from each site was modeled using nonlinear regression applied to an exponential growth model of the form $\text{length} = ae^{Gx}$, where a = length at hatch (y-intercept), x = age in days, and G is the instantaneous growth rate. The exponential growth equations derived from the aged subsamples were rearranged and solved for age (x) given larval length ($x = [\text{Log}_e(\text{length}) - \text{Log}_e(a)]/G$). Ages were estimated for all non-aged larval freshwater drum (Crecco and Savoy 1987b).

Site-level natural mortality rates were estimated with regression analysis using a linear mortality function $\text{Log}_e N_t = \text{Log}_e N_0 - Zt$, where N_t is the number of larval freshwater drum alive at time t , N_0 is the number of larval freshwater drum alive at time t_0 , t = days, and Z is the instantaneous mortality rate. Analysis of covariance (ANCOVA) was used to compare instantaneous mortality rates among sites.

Testing prediction 2 required a multi-step process that included linking water flow travel time from Gavins Point Dam to each of the four sites with back-calculated hatch locations, and egg incubation times for freshwater drum. First, mean channel velocities (m/s) were estimated in five selected areas of the Missouri River between Gavins Point Dam and site 3 (Figure 1). These estimates were based on velocity measurements made during 1997 and 1998 in conjunction with a concurrent Missouri River project. It was necessary to partition the river into discrete velocity areas because mean channel velocities vary greatly along this longitudinal gradient (Slizeski et al. 1982; Dieterman et al. 1996; Young et al. 1997). Mean channel velocity estimates for discrete areas were

converted to km/hr, and distance (km) from Gavins Point Dam to the four study sites was calculated. Given mean channel velocities and distance, time of travel (h) from Gavins Point Dam to each of the study sites could be determined. Time of travel represents the time it takes for a block of water to flow from Gavins Point Dam to each of the study sites. Swedberg and Walburg (1970) determined the incubation period for freshwater drum embryos varied from 36 h at 21°C to 22 h at 25 °C. For this study, 24 h was used as the incubation period because water temperatures during the larval sampling period included values greater than and less than the incubation temperatures determined by Swedberg and Walburg (1970). Sources of larval freshwater drum collected at each site were estimated by calculating travel time (h), back-calculating hatch locations based on daily age estimates, then adding an additional 24 h to account for incubation. For prediction 2, Chi-square analyses were used to compare frequencies of larvae originating from each source among sites for 1997 and 1998.

Age-0 and Age-1 Freshwater Drum

Sampling.-Age-0 freshwater drum from the 1997 and 1998 cohorts were sampled at site 1 - 3 at the same river bends where larval freshwater drum were collected, but individuals were sampled from riprap shorelines. Preliminary sampling in 1996 indicated freshwater drum were more abundant on outside bend riprap areas than other habitat types. Sampling was initiated in mid-October of both years, and was repeated at monthly intervals through December. Replicate outside bends at each site were partitioned into three parts (i.e., sub-reaches) representing the lower, middle, and upper one-third of the bend. Sub-reaches on each outside bend were randomly selected for sampling in October.

In November, one of the two remaining sub-reaches on each outside bend was randomly selected and sampled. In December, the remaining sub-reach was sampled. This sampling protocol was used to prevent resampling sub-reaches that had been sampled in the previous month. Age-0 freshwater drum were collected using pulsed - DC electrofishing (400 - 420 V, 6 - 10 A, single spherical electrode). Sample durations varied between 530 s and 1,825 s depending on length of the sub-reach. Five replicate bends were sampled during all sampling intervals except when site-specific factors (e.g., sand mining, barge traffic) prevented sampling.

Catch per effort (C/f ; number/min of electrofishing) of age-0 freshwater drum and all species on outside bends declined significantly between October and December due to emigration from this habitat (see Results). Similarly, outside bends were not used by age-0 freshwater drum throughout the winter months. Previous Missouri River studies (Hesse and Newcomb 1982, Newcomb 1989) suggested that wing-dike pools were the primary over-winter habitat for fishes. Thus, age-1 freshwater drum were sampled from wing dike pools at sites 1 - 3 during March 1998 and 1999. A deep-water electrofishing apparatus was used to sample fish in these habitats. A 6.1-m-long insulated cable attached to a spherical electrode was suspended from a boom at the front of the boat, and lowered to the bottom. The electrode system was powered with pulsed-DC electrofishing (320-410 V, 6-13 A). The sampling protocol consisted of slowly moving the boat in reverse through all areas of the wing dike pool for 560-2,300 s depending on the size of the pool. Stunned fish would float to the surface beginning 3-5 min after power was initially applied, and remain afloat for several minutes. Fish collected in outside bend

and wing-dike habitats were enumerated after sampling, and all freshwater drum were measured (mm; total length). Freshwater drum less than 200 mm were weighed, individually-coded, then immediately frozen on dry ice.

Age determination and body condition.-In the laboratory, scales of freshwater drum were mounted between glass slides and aged using a microfiche projector (42 X magnification). Age-0 individuals collected from October to December, and age-1 individuals collected in March were distinguished from older age classes by the absence of an annulus. Relative condition (K_n) was used to quantify changes in body condition of freshwater drum among sampling periods. Relative condition was calculated as $K_n = W/W_s$, where W is the weight (g), and W_s is a length-specific standard weight (g) based on the length-weight relationship of age-0 (October-December) and age-1 (March) freshwater drum collected in this study.

Discharge and water temperature.-Missouri River discharge data were obtained from U.S. Geological Survey gauging stations located near Yankton, South Dakota (upstream from the James River), St. Joseph, Missouri, and Kansas City, Missouri (Figure 1). The gauge at Kansas City was located downstream from the Kansas River confluence. The St. Joseph gauge was used to represent seasonal flows for sites 1 and 2, and the Kansas City gauge represented flows at site 3. Daily water temperature was monitored from May through November 1997 and 1998 with continuous-recording water temperature loggers located in sites 2 and 3. A temperature logger was also deployed in site 1 during 1997, but it was vandalized and not replaced in 1998. Daily Missouri River water temperature for site 1 study site was obtained from water treatment and power

generating facilities located near St. Joseph, both of which draw their intake water directly from the Missouri River. Water temperatures from December through April were obtained from the facilities at St. Joseph as well as power generating facilities near sites 2 and 3. Water temperatures in the tailwater of Gavins Point Dam was obtained from the U.S. Army Corps of Engineers for both years (M. Swenson, U. S. Army Corps of Engineers, personal communication).

Statistical analyses.-A three-way ANOVA was used to compare *C/f* of age-0 freshwater drum on outside bends between years (1997, 1998), and among sites (1, 2, 3), and sampling periods (October, November, December). Years and sites were treated as fixed effects in the model. Prediction 3 was tested with regression analysis where site-level density of settling larval freshwater drum was the independent variable, and site-level *C/f* of age-0 freshwater drum in October was the dependent variable. A two-way ANOVA was used to compare *C/f* of age-1 freshwater drum from wing dike pools in March between years and among sites. Individuals included in this analysis represent the 1997 and 1998 cohorts.

A two-way ANOVA was used to compare length, weight, and K_m in October between years and among sites. A nonparametric one-way ANOVA (Kruskal-Wallis test) was used to compare water temperature and discharge among sites and between years for the period spanning initiation of spawning to October sampling. The Kruskal-Wallis test was used because errors for water temperature and discharge were not normally distributed. When significant differences ($P \leq 0.05$) existed in the overall Kruskal-Wallis test, pairwise comparisons were conducted using multiple Wilcoxon 2-sample tests. The

critical probability level ($\alpha = 0.05$) was maintained in multiple comparisons using a Bonferroni adjustment (e.g., $P = \alpha / \text{number of pairwise comparisons}$; Trippel and Hubert 1990). Correlation analysis was used to examine relations between mean length, weight, and K_n of age-0 freshwater drum and October C/f of age-0 freshwater drum, C/f of other taxa, and C/f of all individuals. Emerald shiners *Notropis atherinoides* (a zooplanktivore; Fuchs 1967) and gizzard shad *Dorosoma cepedianum* (a zooplanktivore-omnivore; Dettmers and Stein 1996) were excluded from the latter two analyses because food habits of these species overlap little with food habits of age-0 freshwater drum in the lower Missouri River during the summer growing season (Pflieger 1997).

Prediction 4 was assessed by comparing site-level length-frequency distributions of freshwater drum between October and March using Chi-square analysis. Evidence for size-selective overwinter mortality would include a shift in length-frequencies toward larger lengths in the March collections. Regression analysis was used to test prediction 5 where C/f of age-1 freshwater drum in March was the dependent variable and C/f of age-0 freshwater drum in October was the independent variable. Site-level changes in K_n between October and March were compared using t-tests.

Results

Larval Freshwater Drum

Water temperature and discharge.-Water temperature in the Missouri River differed between years during larval collection periods. In 1997, water temperature

reached 18°C on June 4 at Gavins Point Dam, and June 3 in the channelized river (Figure 2). An early warming trend occurred in 1998, and water temperature reached 18°C on May 17 (Gavins Point Dam) and May 7 (channelized river). Mean water temperature during the spawning season was similar between years at Gavins Point Dam (21.3°C-22.0°C) and the channelized river (24.1°C - 25.2°C). Spawning water temperatures were interrupted at Gavins Point Dam in 1997 and 1998 during two time intervals when water temperature declined to less than 18°C (Figure 2). Water temperature at Gavins Point Dam was more variable in 1998 (coefficient of variation, CV = 17.7) than 1997 (CV = 13.6). Water temperature in the channelized river remained at or above 18°C during the larval sampling periods, and was more variable in 1998 (CV = 14.1 - 14.9) than 1997 (CV = 11.8 - 11.9).

Discharge (m^3/s) during the larval sampling period varied between years at Gavins Point Dam and the channelized river (Figure 3). Discharge releases from Gavins Point Dam were about two times greater and less variable in 1997 (mean = 1,720 m^3/s , CV = 1.71) than 1998 (mean = 830 m^3/s , CV = 10.54) for the period following the initial temperature rise to 18 °C. In the channelized river, discharge was also higher and less variable in 1997 (St. Joseph, mean = 2,407 m^3/s , CV = 10.0; Kansas City, mean = 2,621 m^3/s , CV = 11.1) than 1998 (St. Joseph, mean = 2,050 m^3/s , CV = 30.9; Kansas City, mean = 2,339 m^3/s , CV = 25.0). Two high-discharge events occurred in 1998 (mid-June, early July), whereas a single period of high discharge occurred in 1997 during late June (Figure 3).

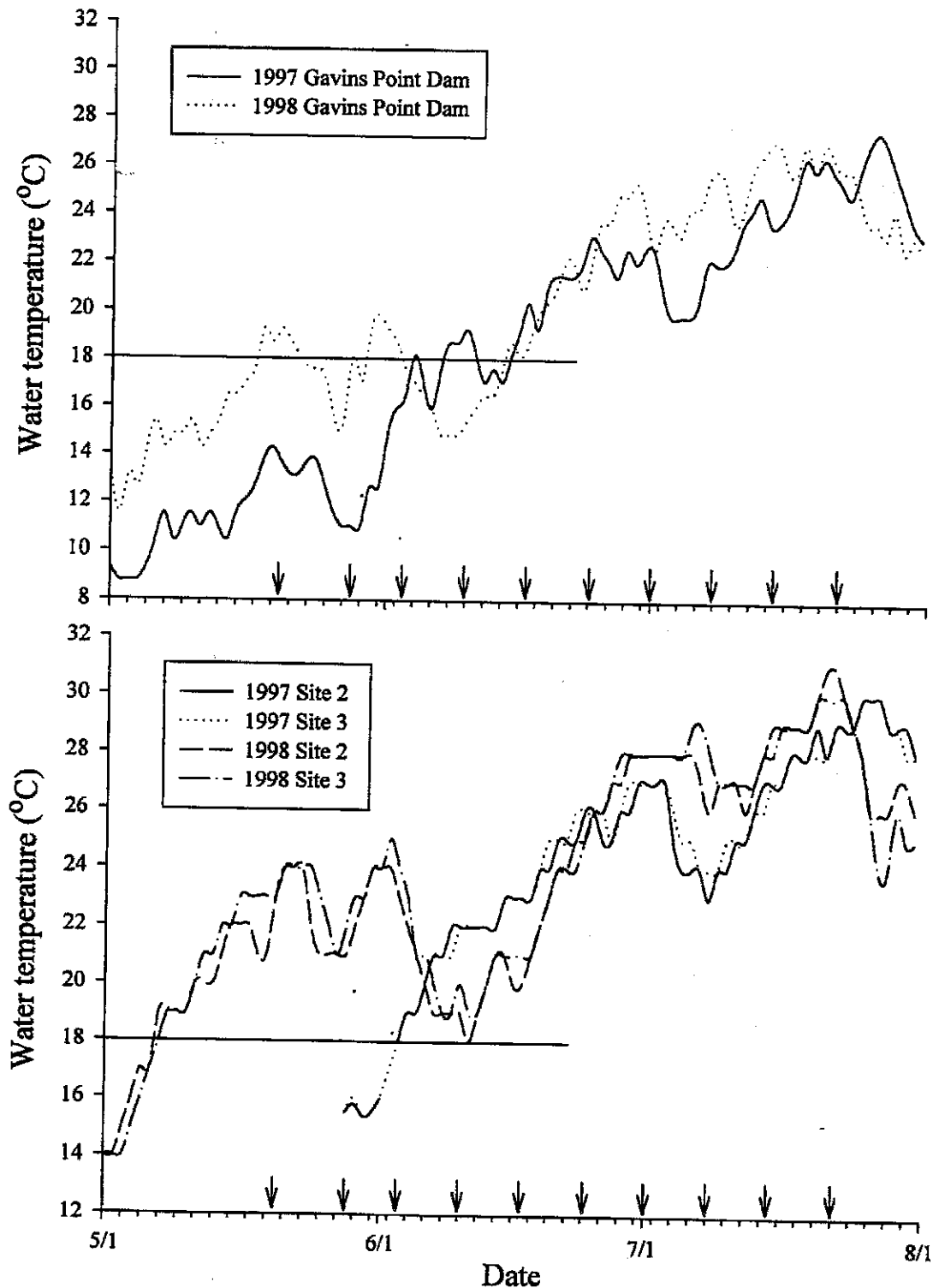


Figure 2.-Water temperature (°C) at Gavins Point Dam (top panel) and in the channelized Missouri River at sites 2 and 3 (bottom panel) from May through July in 1997 and 1998. Arrows represent larval freshwater drum sampling dates. Solid horizontal line indicates water temperature (18°C) which initiates spawning in freshwater drum.

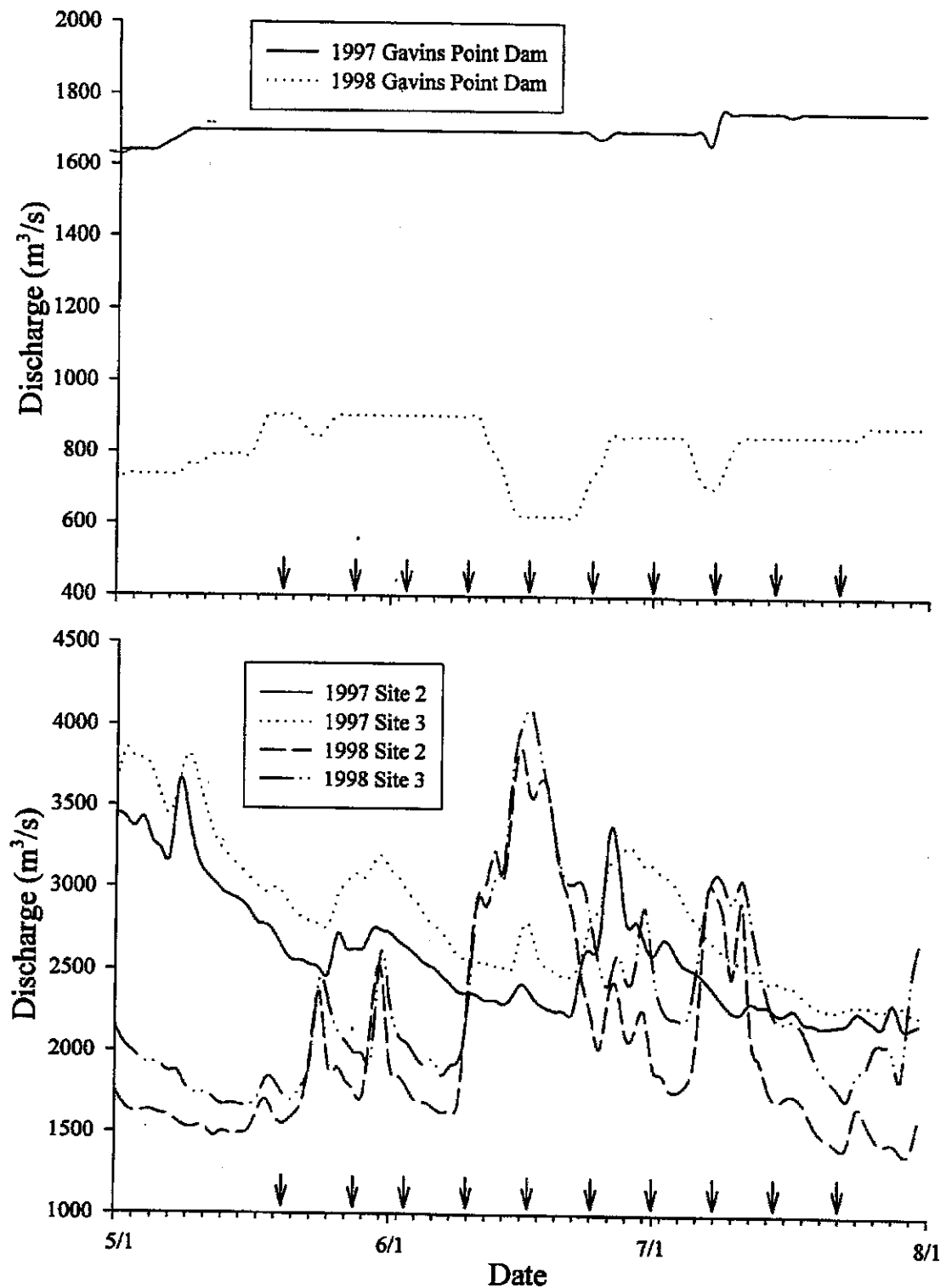


Figure 3.-Discharge (m^3/s) at Gavins Point Dam (top panel) and in the channelized Missouri River at sites 2 and 3 (bottom panel) from May through July in 1997 and 1998. Arrows represent larval freshwater drum sampling dates.

Spatial and temporal abundance of larval freshwater drum.-Larval sampling varied between years and was dependent on water temperatures nearing 18°C (spawning threshold). In 1997, sampling started on May 27 when water temperature was 14.6°C - 15.8°C in the channelized river, and 11.1°C at Gavins Point Dam (Figure 2). Following the onset of an early warming trend in 1998, sampling was initiated on May 19 at water temperatures 22.5 - 23.8°C in the channelized river, and 18.9°C at Gavins Point Dam.

A total of 3,964 freshwater drum were collected in 1997. Length was measured on 3,893 individuals, and all except one were larvae (i.e., < 16 mm). Length measurements were obtained on 5,004 of 5,021 freshwater drum collected in 1998, and 96% were larvae.

Larval freshwater drum were first collected in 1997 on June 16 at all sites, but in low abundance ($N = 19$). Initial appearance of the larvae occurred approximately 12 days after water temperature reached 18°C. Density of larval freshwater drum differed significantly among sampling periods ($F = 33.71$, $df = 5, 96$, $P = 0.0001$). Density was low through June 17, increased significantly ($P = 0.0001$) during June 24 and July 1, then declined during the remaining sampling periods (Figure 4). Eighty-six percent of the larval freshwater drum were collected during the June 24 and July 1 sampling periods. Density of larval freshwater drum marginally differed among sites ($F = 2.53$, $df = 3, 96$, $P = 0.06$). In general, the highest larval density was at the reference site (Figure 4).

Periods of high discharge in 1998 hindered the collection of larval fish samples. A single replicate was collected at the reference site and site 1 during June 10 as a result of increasing discharge (Figure 3) and dangerous woody debris loads in the Missouri

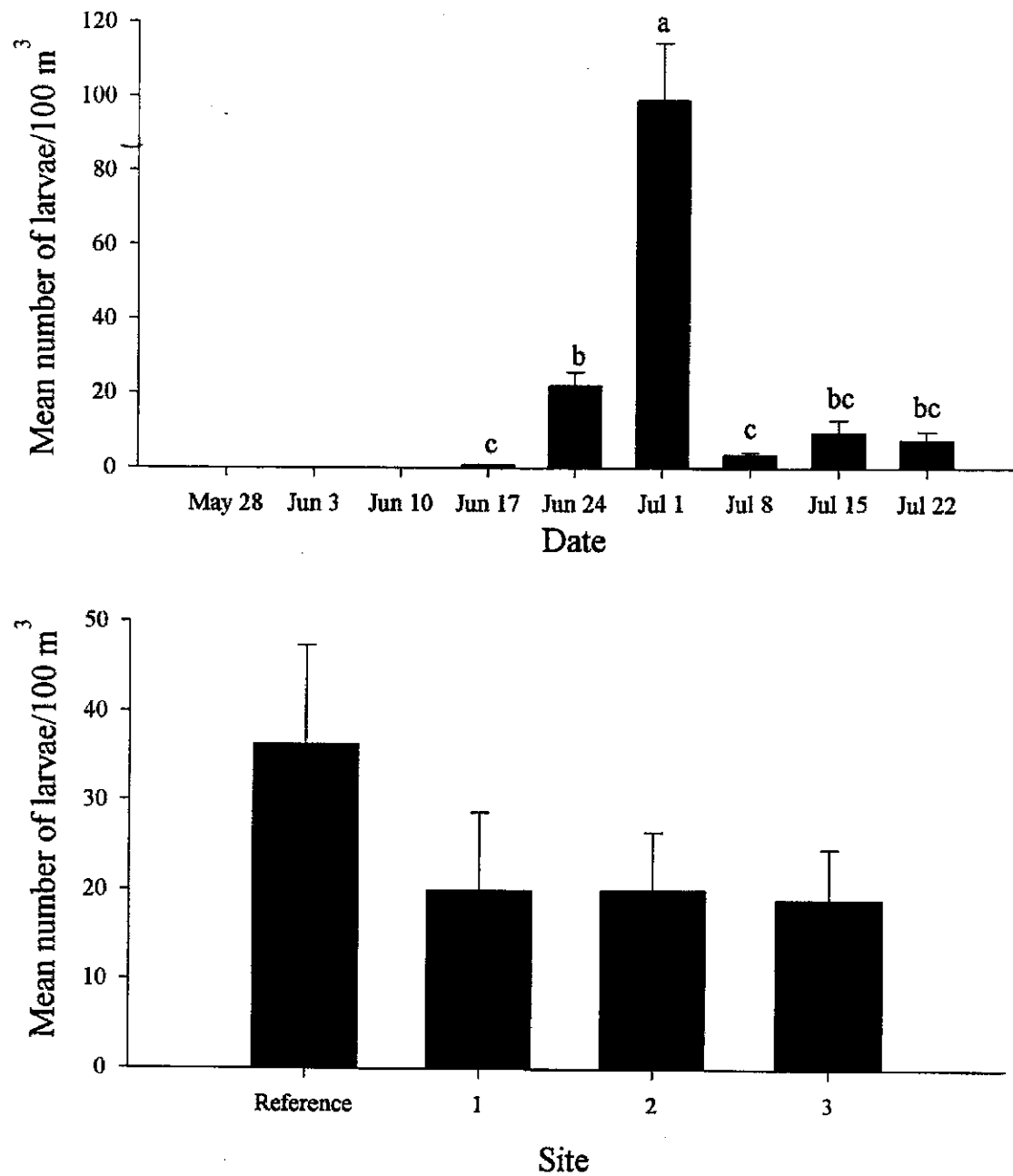


Figure 4.-Mean density ($\pm 1SE$) of larval freshwater drum collected in 1997 on nine dates (top panel) at four sites (bottom panel) in the channelized Missouri River. Bars with the same letter are not significantly different ($P > 0.05$).

River. Although discharge was similarly high at sites 2 and 3, three replicate samples were collected at these sites because the woody debris load was not present. No larval fish samples could be collected at site 2 on June 18 and June 24 because of flooding.

First collections of larval freshwater drum at all sites in 1998 did not occur until June 3 despite the early temperature rise to 18°C between May 7 (channelized river) and May 17 (Gavins Point Dam). Similar to 1997, 88% of the larval freshwater drum collected in 1998 were collected during the June 24 and July 1 sampling periods. Densities of larval freshwater drum in 1998 differed among sampling periods ($F = 19.85$, $df = 7, 55$, $P = 0.0001$) and sites ($F = 4.59$, $df = 3, 55$, $P = 0.006$), but there was a significant sampling period \times site interaction ($F = 4.89$, $df = 19, 55$, $P = 0.0001$). Partitioned sums of squares and 1 df contrasts indicated significant ($P < 0.0001$) sampling period \times site interactions spanning the June 24 through July 8 sampling periods (Figure 5). Mean density of larval freshwater drum between June 24 and July 1 increased 6 times at site 3, 111 times at site 1, and 91 times at the reference site. Density did not differ ($P > 0.05$) among sites during June 24, but was significantly higher ($P < 0.0001$) at site 1 and the reference site on July 1. Mean density from July 1 to July 8 decreased 99% (reference site), 99.5% (site 1), 92% (site 2), and 31% (site 3). In addition, mean density did not differ significantly among sites on July 8 ($P > 0.05$).

Mean density of larval freshwater drum during the period of peak abundance (July 1 in both years) differed significantly between years ($F = 18.85$, $df = 1, 24$, $P = 0.0002$) and among sites ($F = 9.95$, $df = 3, 24$, $P = 0.0002$). Mean density was higher in 1998 (324 larvae/100 m³) than 1997 (99 larvae/100 m³), and declined from 299 larvae/100 m³

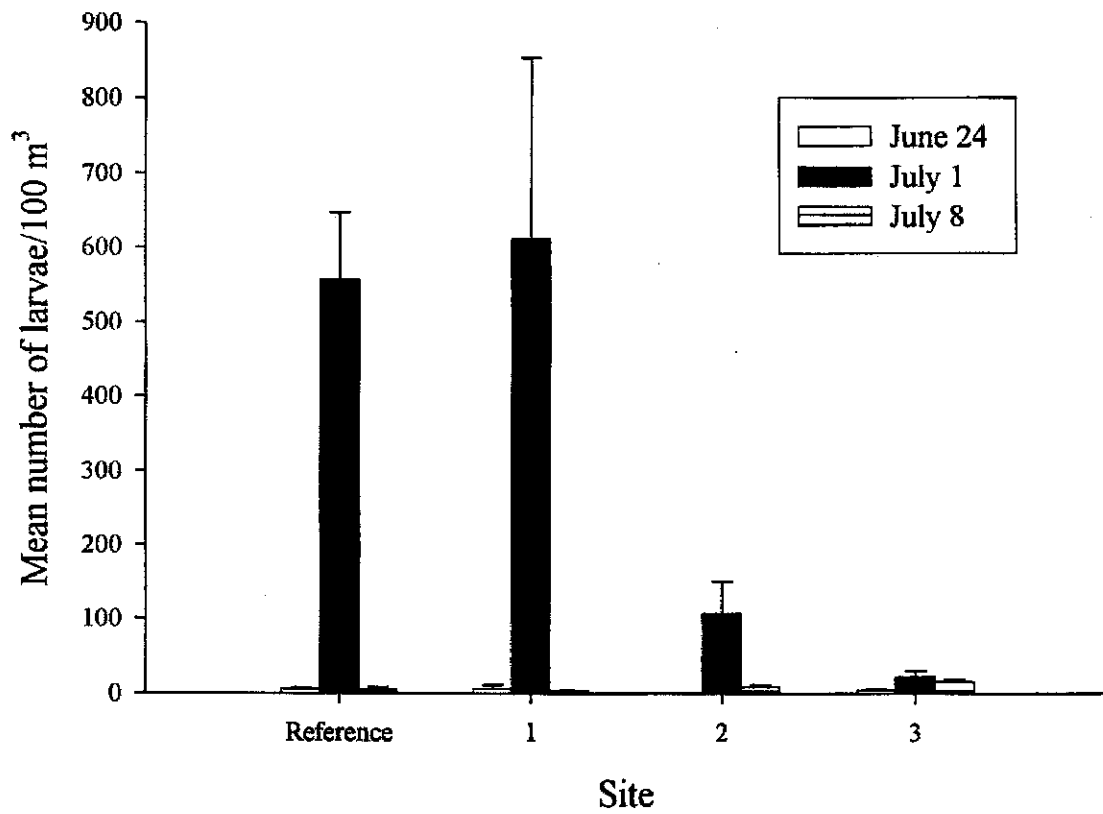


Figure 5.-Mean density (± 1 SE) of larval freshwater drum sampled in 1998 at four sites in the channelized Missouri River on June 24, July 1, and July 8. No samples were made at site 2 on June 24 due to flooding.

at the reference site to 51 larvae/100 m³ at site 3; however, there was a significant year x site interaction ($F = 7.25$, $df = 3, 24$, $P = 0.001$; Figure 6). One df contrasts indicated peak densities of larval freshwater drum increased significantly more ($P < 0.0001$) in 1998 relative to 1997 at the reference site and site 1 than site 2; density declined at site 3. Peak density was similar (P -values > 0.66) between years at sites 2 and 3, but significantly greater (P -values ≤ 0.0006) during 1998 at site 1 and the reference site (Figure 6).

In 1997, there was a weak ($P = 0.064$, $r^2 = 0.18$) negative relationship between site-level densities of larval freshwater drum and distance downstream from Gavins Point Dam (Figure 7); whereas, in 1998 there was a strong and highly significant ($P = 0.001$, $r^2 = 0.68$) negative relationship (Figure 7).

Growth of freshwater drum.-Mean length of freshwater drum differed between years. Mean length of all freshwater drum collected (larval and juveniles) was significantly greater ($P < 0.0001$) in 1998 (median = 9.0 mm, 25 - 75% quartiles = 7.8 - 10.4 mm, $N = 5,004$) than 1997 (median = 4.2 mm, 25 - 75% quartiles = 3.9 - 4.6 mm, $N = 3,893$). Similarly, mean length of larval freshwater drum (i.e., < 16 mm) was significantly greater ($P < 0.0001$) in 1998 (median = 8.9 mm, 25 - 75% quartiles = 7.8 - 10.2 mm, $N = 4,796$) than 1997 (median = 4.2 mm, 25 - 75% quartile = 3.9 - 4.6 mm, $N = 3,892$).

Ages of larval freshwater drum varied from 1 to 21 days (3.14 - 15.2 mm) in 1997, and 2 - 23 days (3.48 - 15.8 mm) in 1998. Exponential models adequately described length-at-age relationships (r^2 -values > 0.84) at all sites in both years (Table 1).

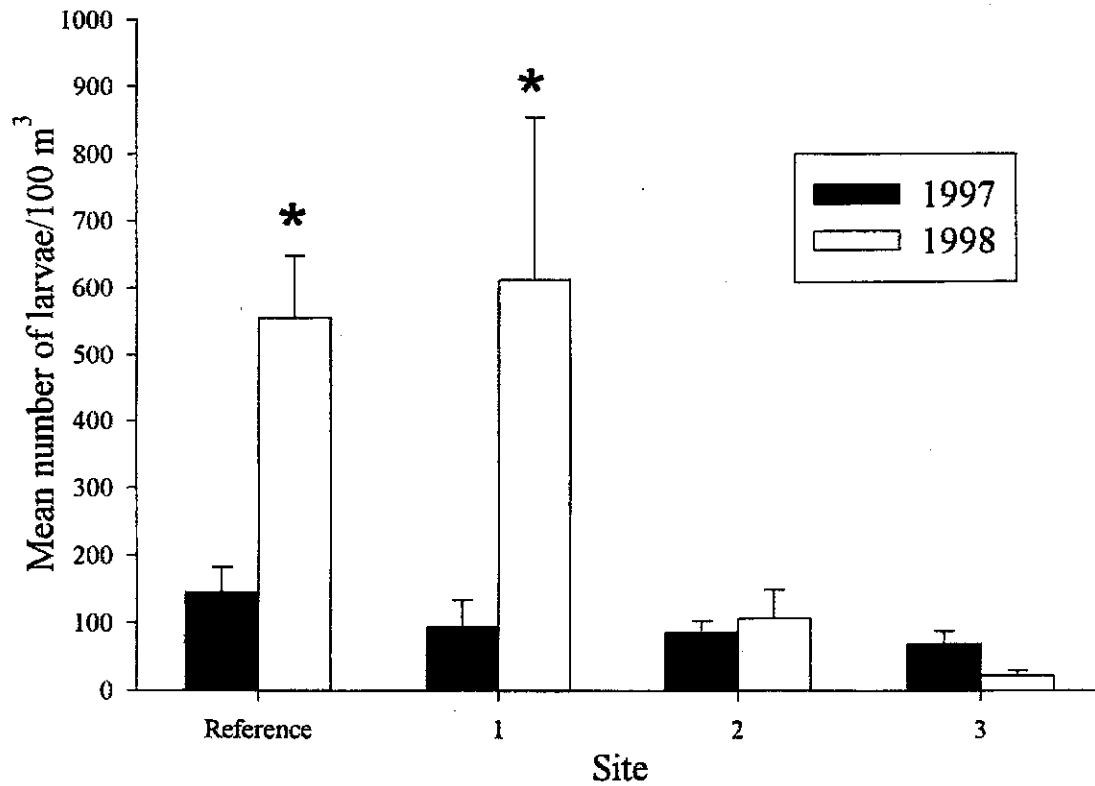


Figure 6.-Mean density ($\pm 1SE$) of larval freshwater drum collected in 1997 and 1998 at four sites in the channelized Missouri River during peak abundance (July 1). Asterisk denotes significant differences ($P < 0.05$) in larval density within a site.

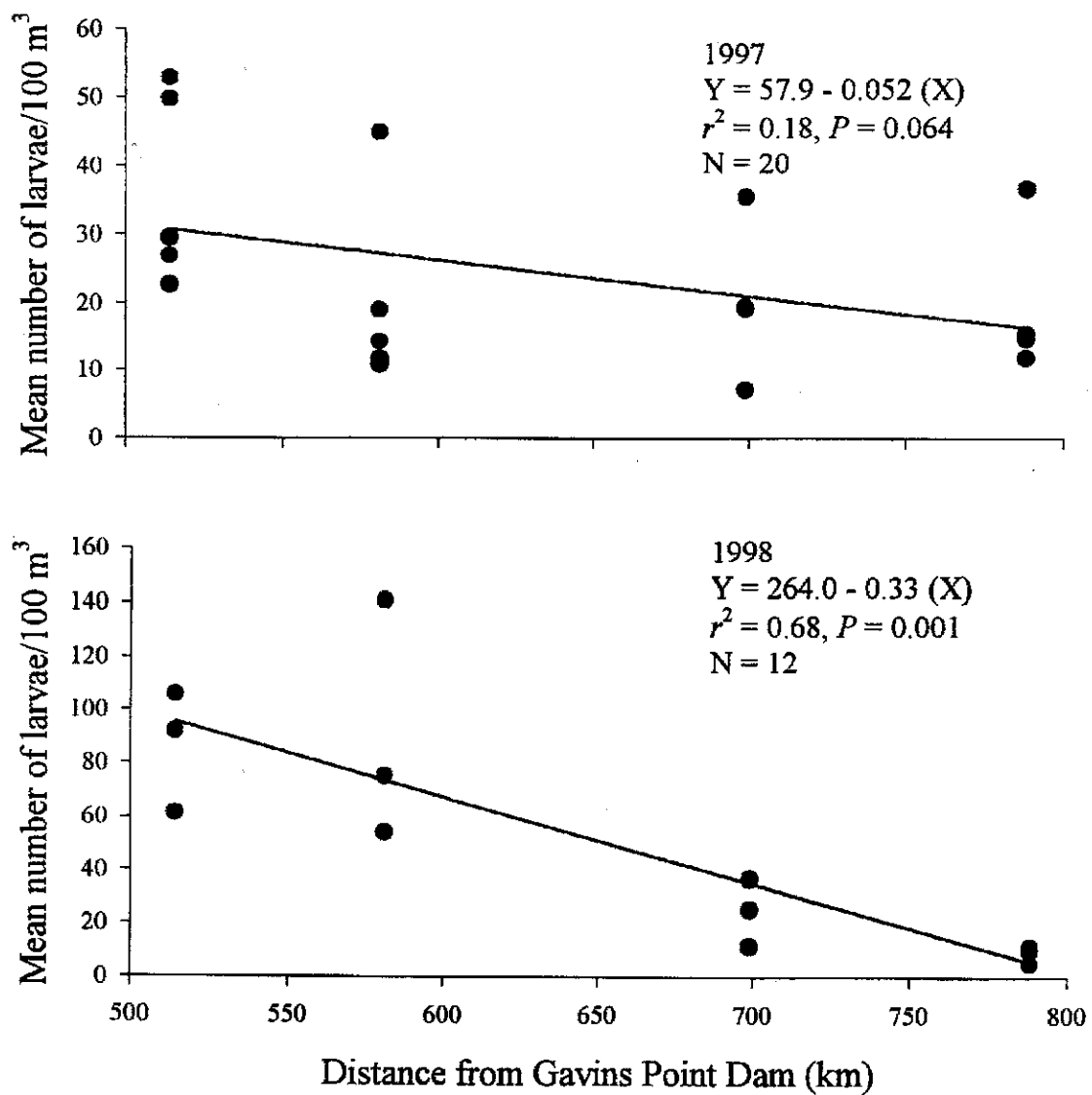


Figure 7.-Relationships between mean density of larval freshwater drum (number/100 m³) collected at four sites in the channelized Missouri River and distance from Gavins Point Dam in 1997 (top panel) and 1998 (bottom panel).

Table 1.- Parameter estimates for exponential growth models of larval freshwater drum collected at the reference site, and sites 1, 2, and 3 in the channelized Missouri River during 1997 and 1998. Exponential growth model is length (mm) = ae^{Gx} , where a is the intercept, G is the instantaneous growth rate, and X is age (days). Standard errors (SE) and 95% confidence intervals (95% CI) are asymptotic estimates based on nonlinear estimation.

Year	Variable	Site			
		Reference	1	2	3
1997	Ages	2-17	2-20	2-21	1-20
	Length	3.23-10.45	3.19-14.1	3.26-15.2	3.14-11.51
	N	37	39	43	42
	r^2	0.88	0.90	0.89	0.84
	a (± 1 SE)	3.32 (0.18)	3.10 (0.19)	3.23 (0.18)	3.45 (0.24)
	a 95% CI	2.97-3.69	2.73-3.48	2.86-3.60	2.97-3.93
	G (± 1 SE)	0.070 (0.005)	0.078 (0.005)	0.076 (0.004)	0.066 (0.005)
	G 95% CI	0.060-0.079	0.069-0.087	0.067-0.085	0.056-0.076
1998	Ages	3-22	2-23	2-23	2-23
	Length	3.75-15.1	3.48-15.8	3.5-15.8	3.65-15.6
	N	61	63	62	63
	r^2	0.94	0.95	0.94	0.94
	a (± 1 SE)	3.60 (0.15)	3.81 (0.14)	3.86 (0.16)	3.92 (0.16)
	a 95% CI	3.292-3.898	3.536-4.076	3.547-4.173	3.603-4.245
	G (± 1 SE)	0.068 (0.002)	0.062 (0.002)	0.062 (0.002)	0.060 (0.002)
	G 95% CI	0.063-0.073	0.058-0.066	0.057-0.066	0.055-0.064

Model intercepts (a-values) and instantaneous growth coefficients (G-values) were similar ($P > 0.05$, i.e., overlapping 95% confidence intervals) among sites within years. Thus, pooled exponential growth models were developed by year (Figure 8). Growth of larval freshwater drum was slightly greater in 1997 ($G = 0.072$, 95% CI = 0.068 - 0.077) than 1998 ($G = 0.062$, 95% CI = 0.060 - 0.064). Average incremental increases in length for larvae in 1997 were 0.32 mm (days 1 - 8), 0.57 mm (days 9 - 16), and 0.91 mm (days 17 - 23); whereas, in 1998 increases in length were 0.31 mm (days 1 - 8), 0.51 mm (days 9 - 16), and 0.80 (days 17 - 23).

Spatial and temporal variation in age structure.-Ages of larval freshwater drum collected on June 16 in 1997 varied from zero (prolarvae) to 4 days. Based on a 1-day hatch period, the back-calculated spawning date of the oldest individual was June 11, immediately preceding the decline in water temperatures at Gavins Point Dam (Figure 2). Thus, spawning started 7 - 8 days following the initial water temperature rise to 18°C. Abundance of larval freshwater drum started to increase on June 24 in 1997 (Figure 4), and the age structure was unimodal at all sites (Figure 9). The oldest individual collected was 7 days which corresponded to a spawning date of June 17. The large increase in the abundance of larval freshwater drum on July 1 (Figure 4) had a corresponding broad age distribution at all sites (Figure 9). The maximum age collected was 18 days which coincides with a spawning date of June 12. After the July 1 sampling period in 1997, the age structure of the larval freshwater drum population varied from 0 to 18 days.

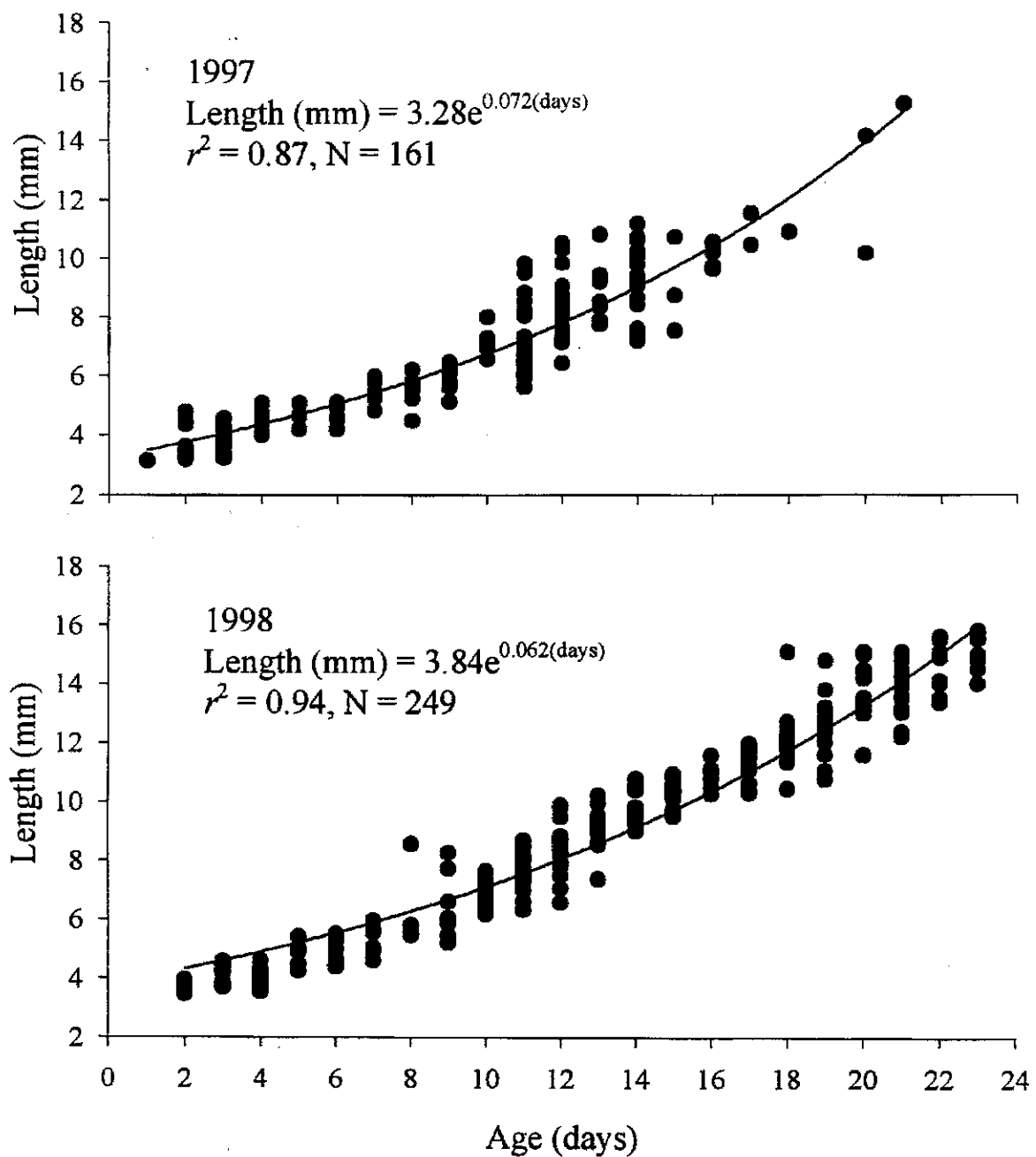


Figure 8.-Exponential growth models for larval freshwater drum collected in the channelized Missouri River during 1997 (top panel) and 1998 (bottom panel).

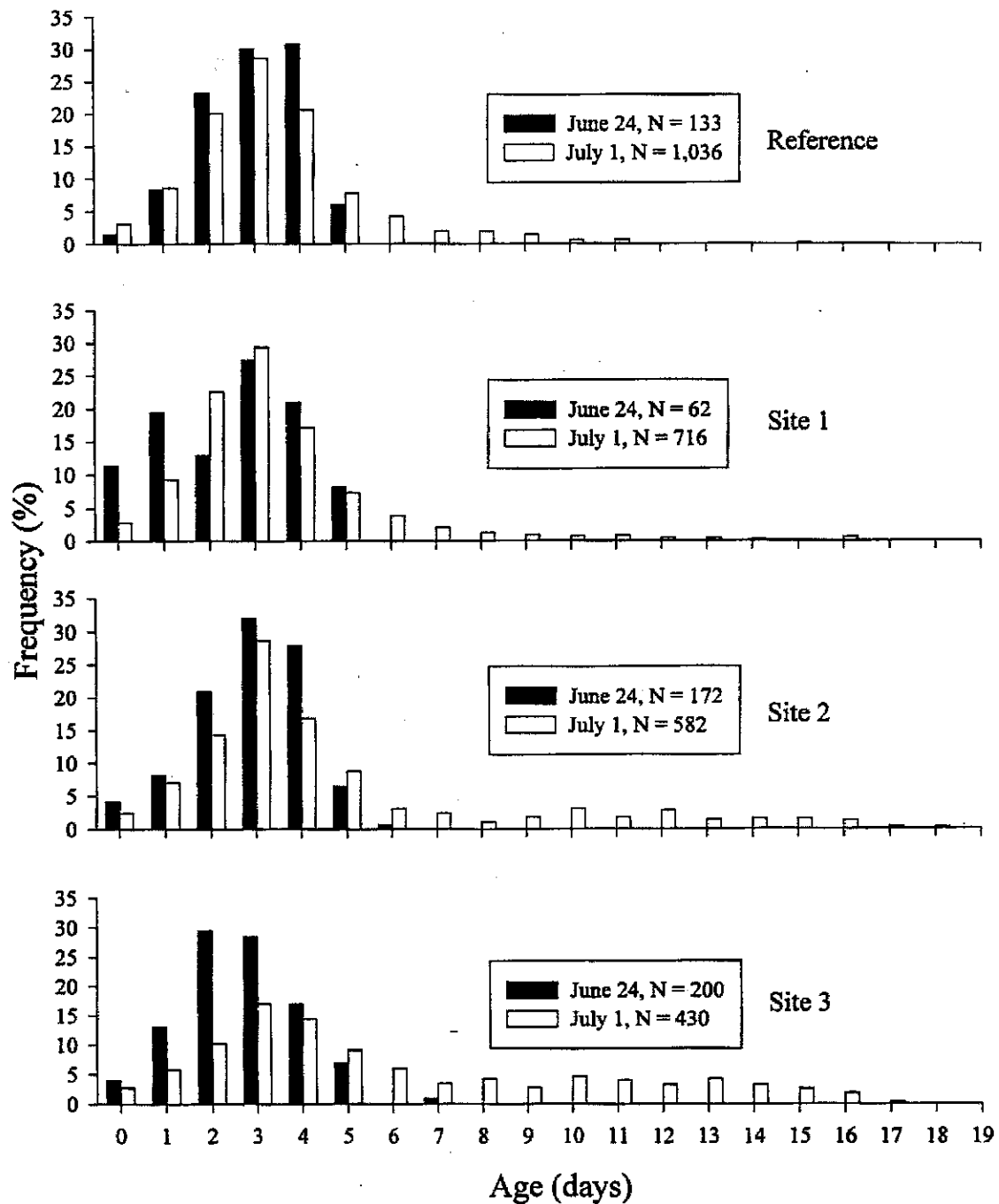


Figure 9:-Age-frequency histograms of larval freshwater drum collected at four sites in the channelized Missouri River during 1997 on June 24 and July 1.

Larval freshwater drum were first collected on June 3 in 1998, and varied from zero to 6 days. Back-calculation of spawning date indicated spawning started on May 28 preceding the second decline in water temperature to less than 18 °C at Gavins Point Dam (Figure 2). Only two fish were collected (ages 7, 12) on June 10 which represent spawning dates of June 3 and May 28. The absence of younger age classes during this collection period suggests spawning was suppressed when water temperatures declined to less than 18°C at Gavins Point Dam. No larval freshwater drum were collected on June 18 following colder water temperatures (< 18°C) during the previous week (Figure 2). Larval freshwater drum were collected in low numbers ($N = 35$) on June 24. Despite suitable spawning temperatures during the ten days prior to June 24 (Figure 2), individuals less than age-5 were dominant in the population (Figure 10). The abundance of larval freshwater drum increased on July 1 (Figure 5), but the age structure was composed primarily of individuals greater than age-9 (Figure 10). Several age classes (e.g, 1-8 days) were absent or present in low numbers.

Age structure of larval freshwater drum differed between years ($P < 0.0001$). Age of larvae collected in 1998 (median age = 14 days, 25 - 75% quartiles = 11 - 16 days, $N = 4,796$) was greater than in 1997 (median age = 3 days, 25 - 75% quartiles = 2 - 5 days, $N = 3,892$).

Settling and natural mortality rates of larval freshwater drum.-Catch curves were used to determine length and age at settling and natural mortality rates of larval freshwater drum (Figure 11). Larval freshwater drum were vulnerable to the gear at 3-days old as evidenced by peak abundance, and the descending limb of the 1997 catch

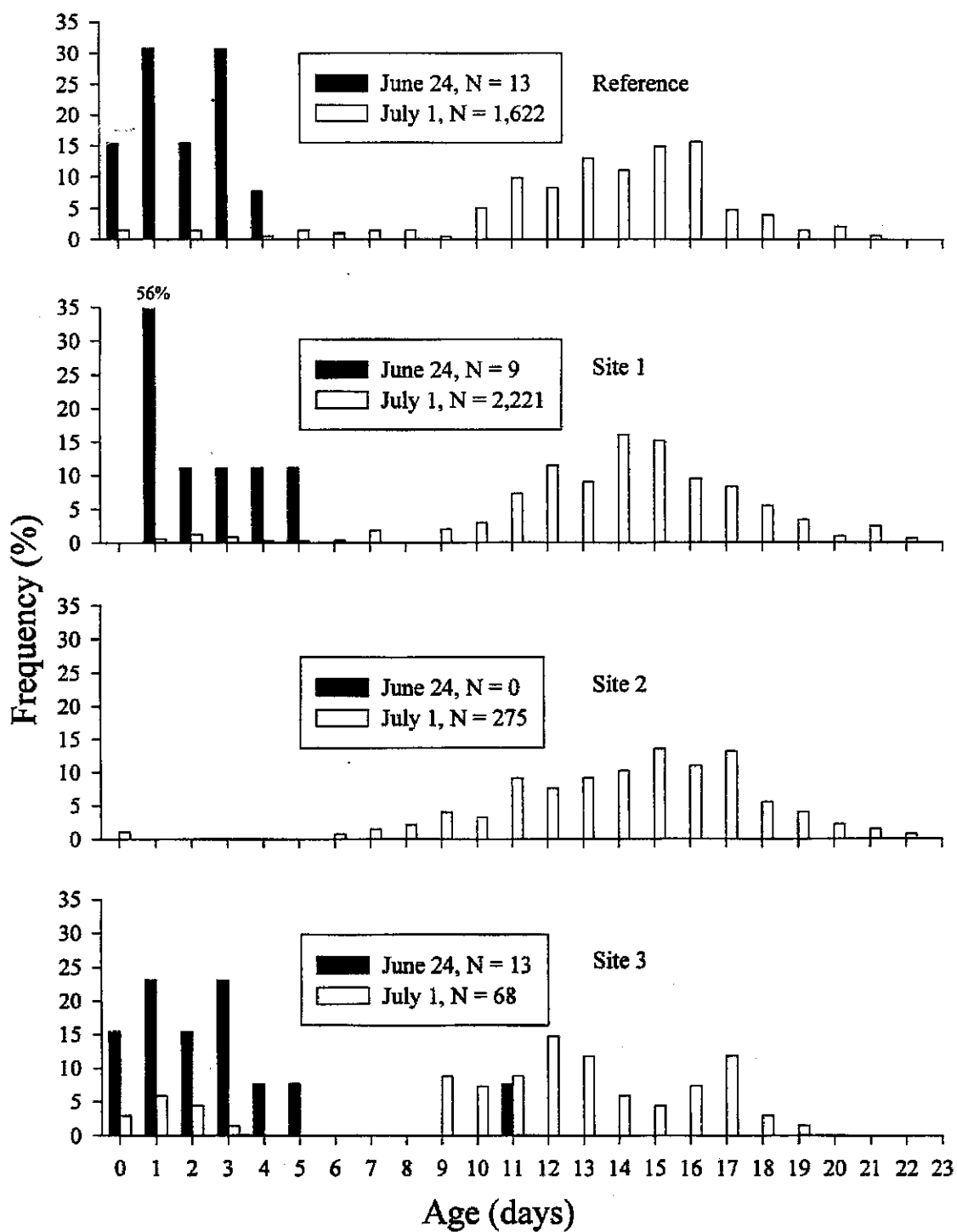


Figure 10.-Age-frequency histograms of larval freshwater drum collected at four sites in the channelized Missouri River during 1998 on June 24 and July 1. No samples were collected at site 2 on June 24 due to flooding.

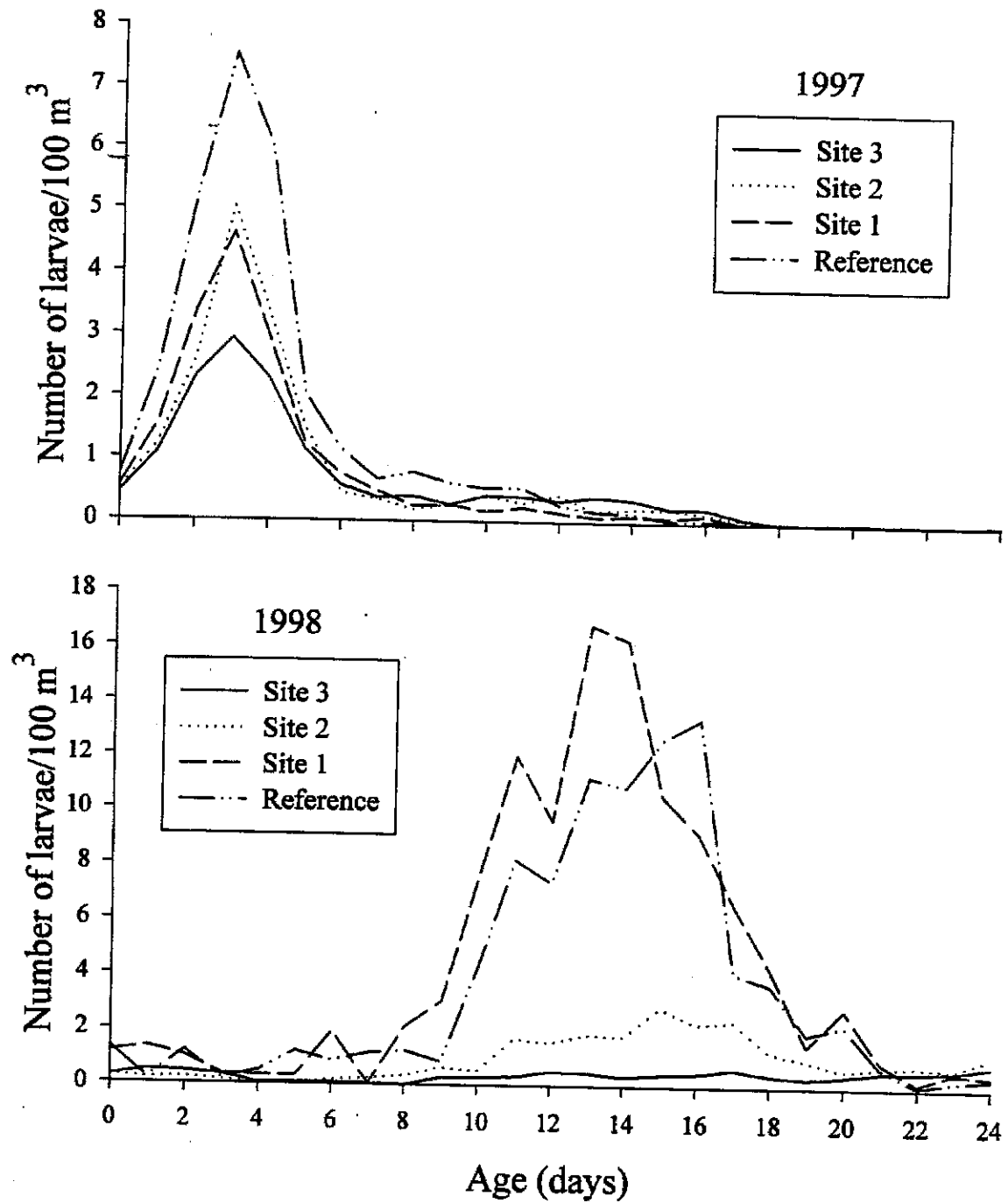


Figure 11.-Density (number/100 m³) at age of larval freshwater drum collected during 1997 (top panel) and 1998 (bottom panel) at four sites in the channelized Missouri River.

curve. In 1997, catch curves for each site were skewed toward older and larger individuals (> 5 days). Catch curves in 1998 were dominated by individuals 10 - 19 days old. The number of larval freshwater drum in 1998 declined rapidly after age 14 (site 1) and age 16 (reference site), and more gradually after age 15 at site 2. No general patterns were evident at site 3 due to the low numbers of larvae collected. These results suggest that settling was occurring between ages 13 and 16 days. Similarly, few larvae greater than 16 mm were collected in 1997. I averaged the age at which peak densities were observed in 1998 at the reference site (16 days), site 1 (13 days), and site 2 (15 days) to obtain an estimate of the average age (mean = 15 days) at which settling is initiated. This age corresponded with a predicted length of 9.70 mm (1997) and 9.73 mm (1998). Instantaneous mortality rates are valid only for larvae less than or equal to 15 days old (i.e., 9.7 mm) to reduce bias associated with losses due to settling.

Catch curves for 1997 (Figure 11) indicate that larval freshwater drum followed a two-stage mortality pattern at all sites. Instantaneous mortality was highest ($Z = 0.56$ - 0.80) among the youngest age classes (3-6 days; Table 2), but did not differ (ANCOVA, $P = 0.41$) among sites.

Instantaneous mortality rates declined for older age classes (7-16 days; Figure 11) in 1997, but a significant mortality model was observed only at the reference site (Table 2). Mortality for the 10-16 day interval could not be estimated for site 1 because insufficient numbers of larval freshwater drum were collected.

Lack of larval freshwater drum less than 9 days old in 1998 (Figure 11) prevented estimation of mortality rates for those age classes. In contrast to 1997, there was an

Table 2.-Instantaneous mortality models for larval freshwater drum at four sites in the channelized Missouri River during 1997. N_t is the number of larval freshwater drum, and t is age in days.

Site	Age interval (days)	P	r^2	Model
Reference	3-6	0.027	0.95	$\text{Log}_e N_t = 6.49 - 0.67t$
	7-14	0.001	0.86	$\text{Log}_e N_t = 3.94 - 0.24t$
1	3-6	0.007	0.99	$\text{Log}_e N_t = 5.78 - 0.63t$
2	3-6	0.024	0.95	$\text{Log}_e N_t = 6.52 - 0.80t$
	7-15	0.116	0.12	$\text{Log}_e N_t = 1.47 - 0.04t$
3	3-6	0.019	0.96	$\text{Log}_e N_t = 5.20 - 0.56t$
	7-15	0.287	0.16	$\text{Log}_e N_t = 1.57 - 0.03t$

abundance of older individuals in 1998 (Figures 10 and 11); however, the descending limb of the catch curves included losses of larvae due to settling. As a result, instantaneous mortality rates could not be calculated for 1998.

Sources of larval freshwater drum.-Differences in discharge between years (Figure 3) influenced channel velocities and estimated flow travel times to the four study sites. In 1997, travel time from Gavins Point Dam was 98 h to the reference site, 109 h to site 1, 134 h to site 2, and 153 h to site 3. During lower discharge in 1998, travel time was 124 h to the reference site, 139 h to site 1, 167 h to site 2, and 187 h to site 3. Differences in travel time between years influenced the age structure of larval freshwater drum reaching each site. Ages of individuals originating from the channelized portions of the Missouri River varied from 0 to 3 days in 1997, and 0 - 5 days in 1998. Larvae originating from the unchannelized Missouri River downstream from Gavins Point Dam varied in age from 2 to 5 days in 1997, and 3-6 days in 1998. In 1997, ages of larvae originating from Lewis and Clark Lake varied from 6 days or greater (site 3) to 4 days or greater (reference site). In 1998, larval freshwater drum from Lewis and Clark Lake were 5 days old or greater at all sites.

The proportion of larval freshwater drum originating from each source differed significantly among sites in 1997 ($P = 0.001$; Figure 12). At the reference site, Lewis and Clark Lake and the unchannelized Missouri River contributed greater than 80% of the larvae collected; whereas, the channelized Missouri River contributed 11%. Each source accounted for 27-40% of the larval freshwater drum sampled at site 1. The channelized Missouri River contributed 48-54% of the larvae collected at sites 2 and 3. In general, the

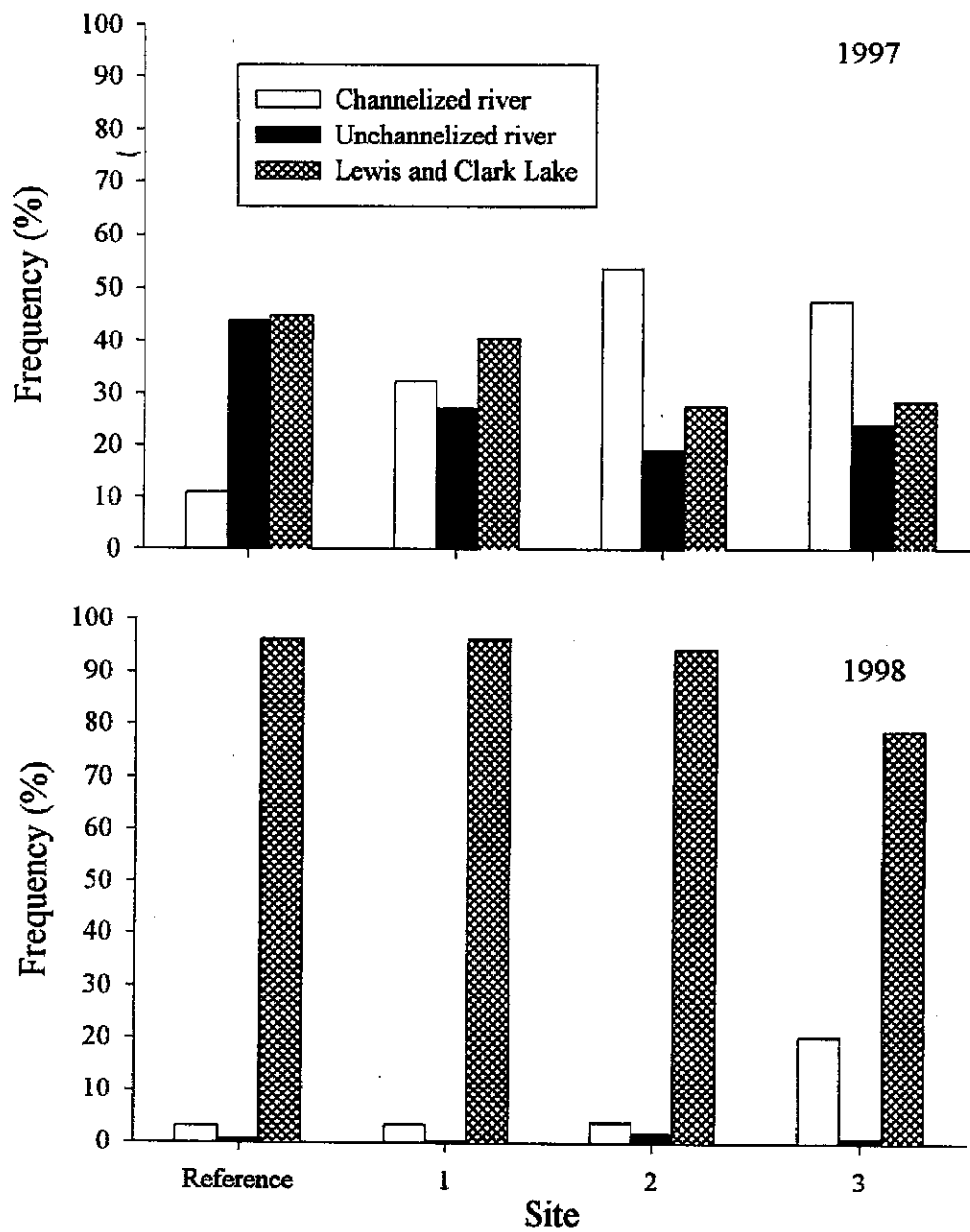


Figure 12.-Site-level frequencies of larval freshwater drum originating from Lewis and Clark Lake, and the unchannelized and channelized Missouri River sources during 1997 (top panel) and 1998 (bottom panel).

number of larval freshwater drum originating in the channelized Missouri River increased from upstream to downstream sites; whereas, contributions from the unchannelized Missouri River and Lewis and Clark Lake decreased from upstream to downstream sites. Averaged across sites, 31% of the larval freshwater drum originated from the channelized river, 32% from the unchannelized Missouri River, and 37% from Lewis and Clark Lake.

The proportion of larval freshwater drum originating from the three sources differed significantly among sites in 1998 ($P = 0.001$; Figure 12). Contributions from the Lewis and Clark Lake source were greater than 78% at all sites. The unchannelized Missouri River contributed less than 2% at all sites. Similar to 1997, the proportion of larval freshwater drum originating from the channelized river increased from upstream to downstream sites, but the channelized river contributed less than 4% of the larval freshwater drum population at all sites except site 3 (20%). Averaged across sites, the proportion of larval freshwater drum originating from the channelized and unchannelized Missouri River, and Lewis and Clark Lake sources in 1998 was 4.1, 0.6, and 95.3%, respectively.

Age-0 and Age-1 Freshwater Drum

Relative abundance.-Freshwater drum was one of the most abundant species collected during the October - March sampling periods, and composed 19.5 - 31.7% of the fishes collected (Table 3). Lengths of freshwater drum collected from sites 1, 2, and 3 during the October 1997 - March 1998 sampling period varied from 61 to 453 mm. The 1997 cohort comprised 92% of the 697 freshwater drum collected, and varied in length from 61 to 181 mm (Figure 13). During the October 1998 - March 1999 sampling period,

Table 3.-Relative abundance (number, % of total) of fishes collected from outside bend and wing dike habitats from 1997 to 1999 during October - March sampling periods in the channelized Missouri River. t = less than 1% of the total number.

Species	1997 - 1998		1998 - 1999	
	Number	%	Number	%
Cyprinidae	2,031	56.7	884	34.7
Freshwater drum	697	19.5	808	31.7
Channel catfish <i>Ictalurus punctatus</i>	271	7.6	80	3.1
Green sunfish <i>Lepomis cyanellus</i>	247	6.9	158	6.2
Gizzard shad	106	2.9	349	13.7
Common carp <i>Cyprinus carpio</i>	62	1.7	18	t
Flathead catfish <i>Pylodictis olivaris</i>	41	1.1	106	4.2
River carpsucker <i>Carpionodes carpio</i>	34	t	19	t
Orangespotted sunfish <i>Lepomis humilis</i>	27	t	82	3.2
White bass <i>Morone chrysops</i>	15	t	2	t
Blue sucker <i>Cycleptus elongatus</i>	8	t	1	t
Rainbow smelt <i>Osmerus mordax</i>	7	t		
Log perch <i>Percina caprodes</i>	6	t	2	t
Black bullhead <i>Ameiurus melas</i>	6	t	1	t
Bluegill <i>Lepomis macrochirus</i>	4	t	12	t
Sauger <i>Stizostedion canadense</i>	4	t	1	t
Smallmouth buffalo <i>Ictiobus bubalus</i>	4	t	2	t
Goldeye <i>Hiodon alosoides</i>	2	t	2	t
Largemouth bass <i>Micropterus salmoides</i>	2	t	1	t
Stonecat <i>Noturus flavus</i>	2	t	1	t
Bighead carp <i>Hypophthalmichthys nobilis</i>	1	t		
Bigmouth buffalo <i>Ictiobus cyprinellus</i>	1	t	2	t
Goldfish <i>Carassius auratus</i>	1	t	10	t
Quillback <i>Carpionodes cyprinus</i>	1	t		
Mosquitofish <i>Gambusia affinis</i>	1	t	4	t
Blue catfish <i>Ictalurus furcatus</i>			2	t
Shortnose gar <i>Lepisosteus platostomus</i>			2	t

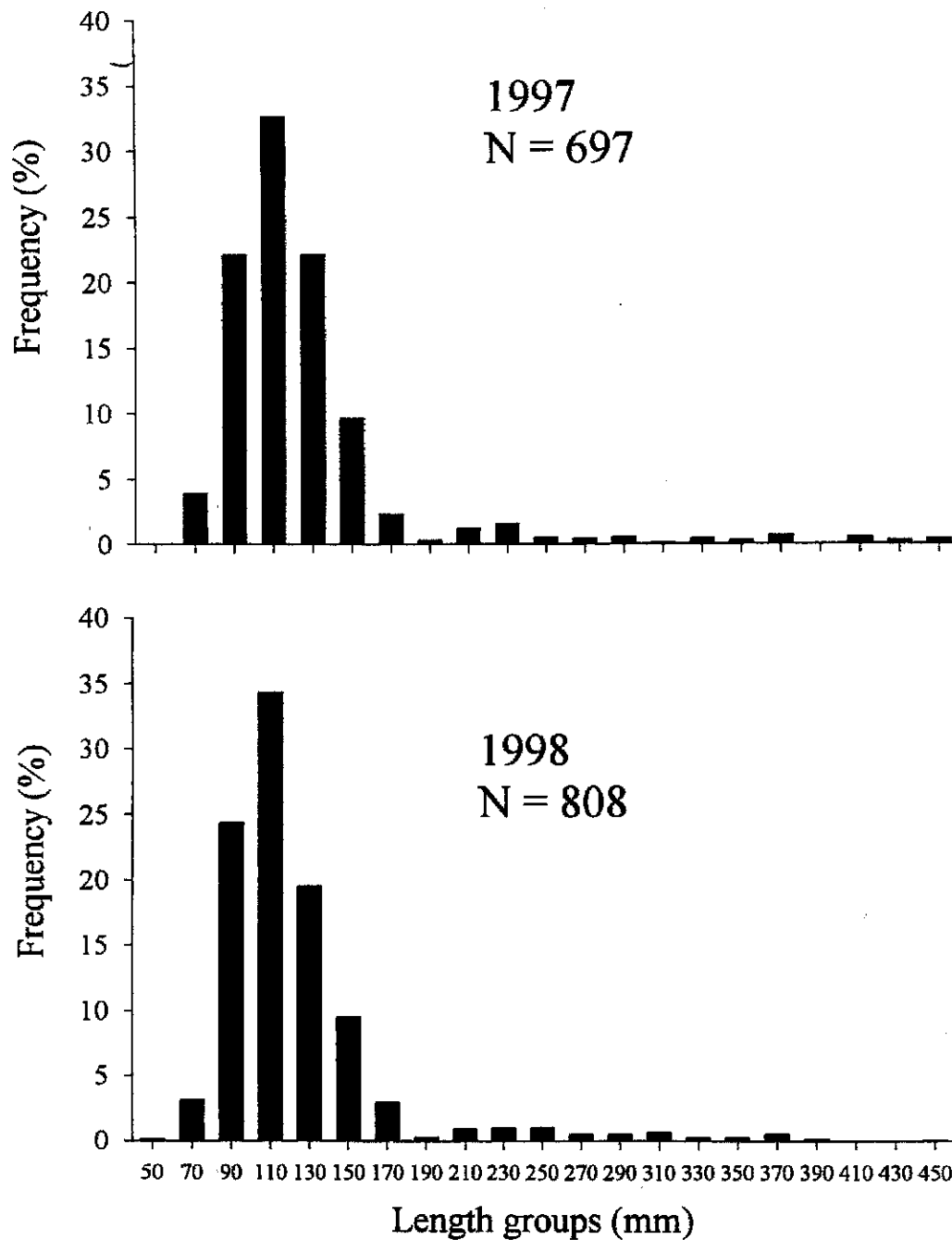


Figure 13.-Length-frequency histograms of freshwater drum collected in the channelized Missouri River during October 1997 - March 1998 (top panel) and October 1998 - March 1999 (bottom panel) at sites 1, 2, and 3.

lengths of freshwater drum varied from 59 to 475 mm. Individuals of the 1998 cohort comprised 94% of the 808 freshwater drum collected, and varied in length from 59 to 186 mm (Figure-13).

Age-0 freshwater drum were abundant on outside bend habitats, but use of this habitat varied spatially and temporally. Catch per effort of age-0 freshwater drum on outside bends differed significantly among months ($F = 58.64$, $df = 2, 63$, $P = 0.0001$). During both years, C/f declined similarly at all sites from October to December (Figure 14). Despite the high abundance on outside bends in October, few age-0 freshwater drum remained in these areas during late fall and early winter. Catch per effort was positively correlated with water temperature in 1997 ($r = 0.89$, $P = 0.0013$, $N = 9$) and 1998 ($r = 0.91$, $P = 0.0006$, $N = 9$). Catch per effort of age-0 freshwater drum was not significantly correlated with discharge in 1997 ($r = 0.58$, $P = 0.09$, $N = 9$) or 1998 ($r = -0.54$, $P = 0.13$, $N = 9$). Although C/f of age-0 freshwater drum on outside bends was about two times greater in 1998 (0.63 ± 0.10 fish/min) than 1997 (0.34 ± 0.08 fish/min), the significant year main effect ($P = 0.0011$) was confounded by a significant year x site interaction ($F = 6.02$, $df = 2, 63$, $P = 0.004$). Partitioned 1 df contrasts indicated a significantly greater ($P < 0.01$) C/f of age-0 freshwater drum at sites 1 and 2 in 1998 than 1997. Catch per effort declined at site 3 in 1998, and was similar to 1997 ($P = 0.49$; Figure 14).

Regression analysis used to test prediction 3 also provided a means to examine the source of the significant year x site interaction in C/f of age-0 freshwater drum. There was a significant positive correlation between densities of settling larvae and October C/f

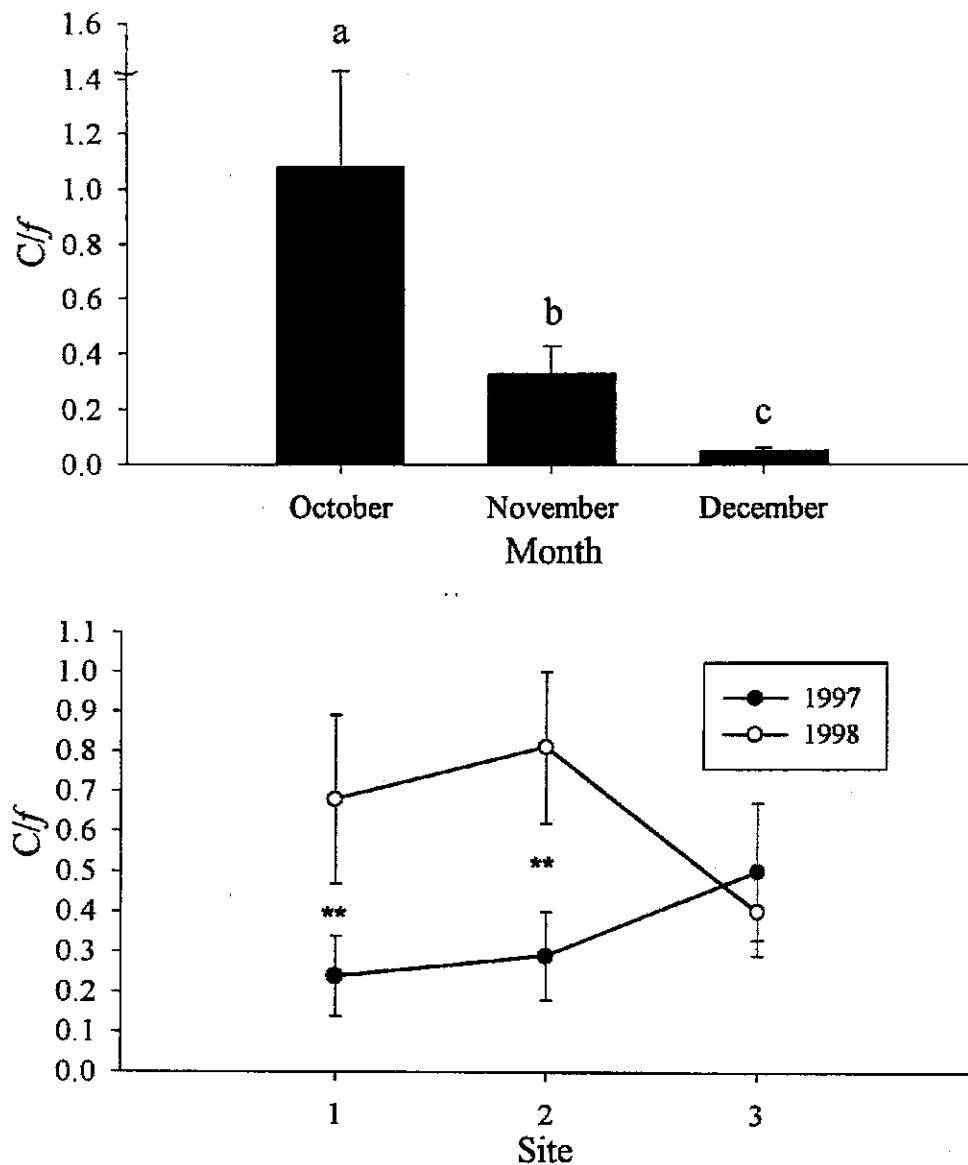


Figure 14.-Mean catch per effort (C/f; number/min; ± 1 SE) of age-0 freshwater drum among months (October, November, December) and sites (1, 2, and 3) in the channelized Missouri River. Mean C/f values are significantly different ($P < 0.05$) among months. Asterisks denote within site differences ($P < 0.05$) in mean C/f between years.

of age-0 freshwater drum in 1997 and 1998 (Figure 15), but slopes differed significantly between years (ANCOVA, $P = 0.0011$). Although larval settling density was 251 times greater in 1998 (mean = 20.4 larvae/100 m³) than 1997 (mean = 0.082 larvae/100 m³), C/f of age-0 freshwater drum in October was only 1.57 times greater in 1998 (mean = 1.32 age-0 freshwater drum/min) than 1997 (mean = 0.84 age-0 freshwater drum/min). The significant year x site interaction in age-0 C/f was dependent on the spatial pattern of larval settlers. Densities of settling larvae and C/f increased from upstream to downstream sites in 1997, but were lower at site 3 than sites 1 and 2 in 1998.

Pre-winter water temperature, discharge, size structure, weight, and body condition.-Water temperature between spawning and October sampling did not differ significantly among sites or between years ($P = 0.13$). Median water temperature varied from 24.8°C to 26.1°C during summer months in both years. Missouri River discharge differed significantly among sites and between years ($P = 0.0001$). Median discharge in 1997 was similar ($P > 0.05$) among sites 1 and 2 (2,247 m³/s) and site 3 (2,278 m³/s), but significantly greater ($P = 0.0001$) at site 3 (2,006 m³/s) than sites 1 and 2 (1,497 m³/s) in 1998.

Mean length of age-0 freshwater drum in October differed significantly between years ($F = 6.1$, $df = 1, 24$, $P = 0.021$) and among sites ($F = 17.99$, $df = 2, 24$, $P = 0.0001$). Mean length (± 1 SE) of the 1997 cohort (115 ± 2.2 mm) was greater than the 1998 cohort (mean = 109 ± 2.4 mm), and was significantly greater ($P < 0.0001$) at site 1 (121 ± 1.9 mm) than site 2 (109 ± 2.7 mm) and site 3 (106 ± 1.4 mm).

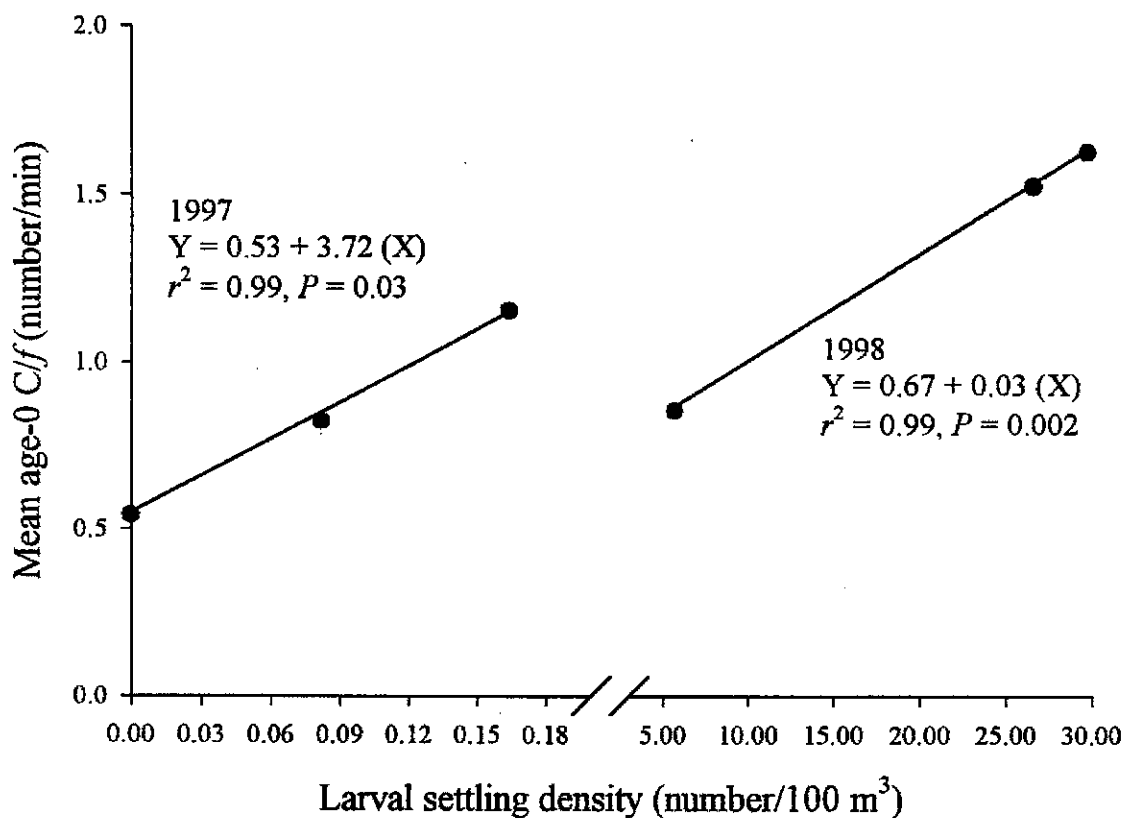


Figure 15.-Relations between site-level densities of settling freshwater drum (≥ 15 days) and site-level catch per effort (C/f) of age-0 freshwater drum in October for the 1997 and 1998 cohorts sampled in the channelized Missouri River. Note break in the abscissa and change in scale between years.

Mean weight of age-0 freshwater drum in October did not differ significantly between years ($P = 0.13$; 1997 mean = 16.6 g, 1998 mean = 14.9 g), but was significantly different among sites ($F = 18.9$, $df = 1, 23$, $P = 0.0001$). Similar to length, mean weight was significantly greater ($P \leq 0.0002$) at site 1 (20.3 ± 1.0 g) than site 2 (14.5 ± 1.1 g) and site 3 (12.5 ± 0.5 g).

Length and weight of the 1997 and 1998 cohorts of freshwater drum were highly correlated ($r = 0.99$, $P < 0.0001$, $N = 1,397$). The lack of correlation between K_n and fish length ($r = 0$, $P = 0.93$, $N = 1,397$) indicated the equation was not length-biased. Relative condition of age-0 freshwater drum in October differed significantly between years ($F = 22.58$, $df = 1, 23$, $P = 0.0001$) and among sites ($F = 7.57$, $df = 2, 23$, $P = 0.003$), and was greater in 1998 (mean = 107 ± 1.03) than 1997 (mean = 101.6 ± 0.92). Mean K_n was significantly greater ($P < 0.03$) at site 1 (107.1 ± 1.6) than site 2 (103.9 ± 1.38) and site 3 (101.7 ± 0.76).

The effects of fish relative abundance on length, weight, and condition of age-0 freshwater drum varied between years. There were no significant relationships ($P > 0.05$) between mean length, weight, and K_n in October and C/f of age-0 freshwater drum. However, in 1997 there were significant negative correlations between mean length, mean weight, and mean K_n of age-0 freshwater drum, and C/f of all fish (age-0 freshwater drum and other benthic insectivores; Figure 16). However, growth indices were not significantly correlated (P -values > 0.67 , r -values < 0.12) with C/f of all fish in 1998.

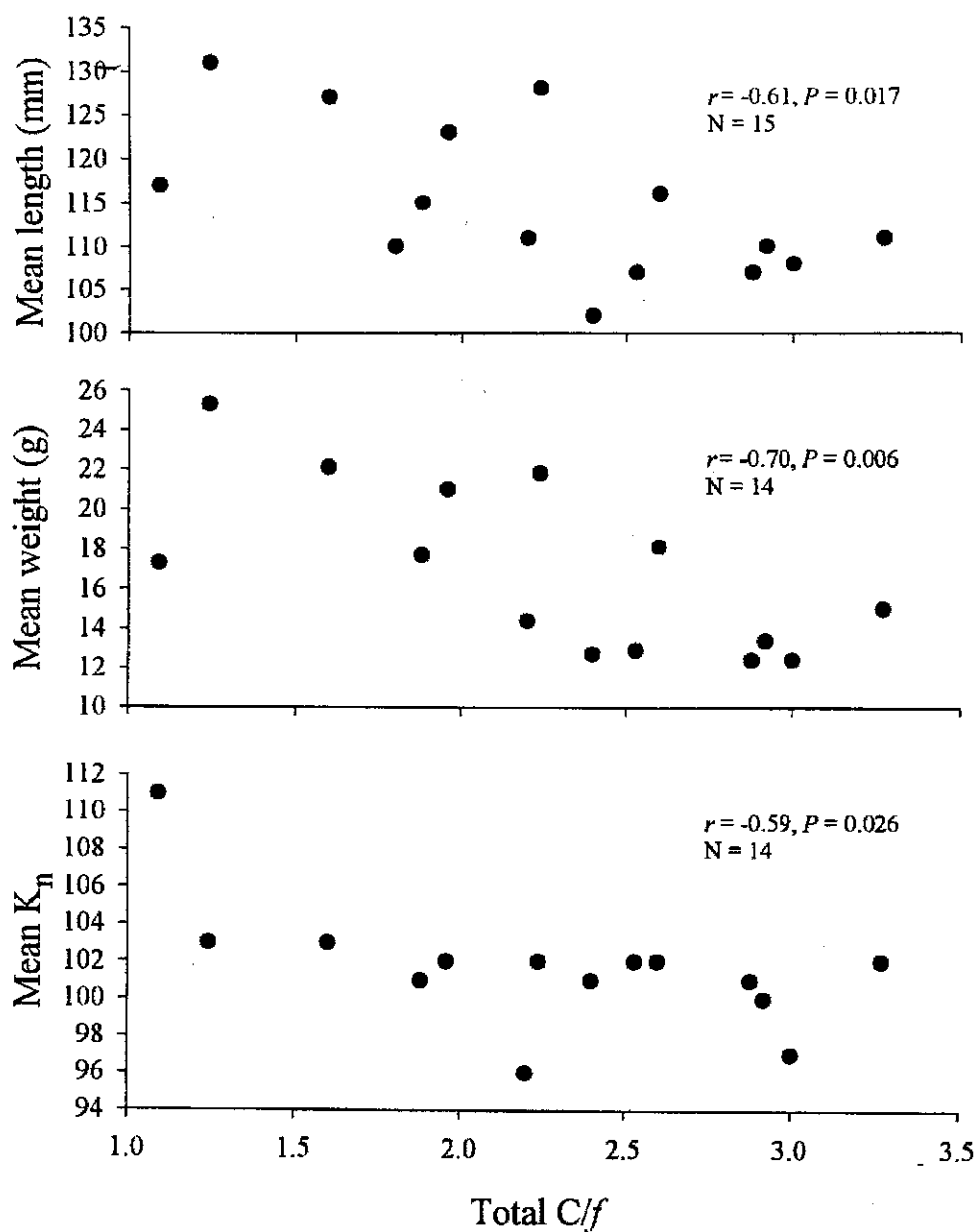


Figure 16.-Correlations between mean length, weight, and relative condition (K_n) of age-0 freshwater drum in October 1997 and total catch per effort (C/f, number/min; age-0 freshwater drum and other benthic insectivores) in the channelized Missouri River.

Overwinter mortality.-Assessment of overwinter mortality and changes in length, and K_n through winter were restricted to comparisons between October and March because significant declines in C/f of age-0 freshwater drum from October to December (Figure 14) were influenced by size-related emigration. For example, mean length in 1997 decreased 2 - 19 mm between October and November at all sites. A similar size-related emigration occurred between October and December 1998, and mean length decreased 12 - 43 mm.

Winter water temperature conditions varied between years. Mean water temperature between October 1997 and March 1998 sampling periods was 4.7°C (site 1), 4.9°C (site 2), and 5.2°C (site 3); whereas, mean water temperature between October 1998 and March 1999 sampling periods was 7.1°C (site 1) and 6.8°C (site 2) and 6.8°C (site 3). There were 70-86 days where water temperature was at or below 4°C during the 1997-1998 winter, but only 48-56 days for the 1998-1999 winter. Degree-days at or below 4°C varied between 94 - 162 during 1997-1998 winter, and 80 - 106 for the 1998-1999 winter. The number of days where water temperature was at or below 1°C varied between 14 - 28 in 1997, and 5 - 20 in 1998.

Relative condition of freshwater drum declined significantly between October and March at all sites during both years, except site 3 during the 1998-1999 winter (Table 4). Mean K_n decreased 15% (site 1), 9% (site 2), and 9% (site 3) during the 1997-1998 winter. During the 1998-1999 winter, mean K_n declined 9% (site 1) and 10% (site 2), but was the same at site 3.

Table 4.-Overwinter changes in mean K_n (standard deviation in parenthesis) for the 1997 and 1998 cohorts of freshwater drum at sites 1, 2, and 3 in the channelized Missouri River. Mean K_n between months within cohorts differed significantly (t-tests, $P < 0.05$) at all sites, except the 1998 cohort at site 3.

Site	1997 cohort		1998 cohort	
	October 1997	March 1998	October 1998	March 1999
21	103 (7.4) $N = 76$	88 (6.5) $N = 114$	110 (9.0) $N = 192$	100 (7.9) $N = 66$
22	101 (8.3) $N = 103$	92 (4.4) $N = 19$	107 (8.5) $N = 208$	96 (10.4) $N = 79$
23	100 (7.5) $N = 141$	91 (9.7) $N = 100$	103 (7.5) $N = 99$	103 (7.3) $N = 6$

There were no significant differences in length-frequency distributions of the 1997 cohort of freshwater drum between October and March at all sites (Figure 17). Increases in mean length between October and March were small, and varied from zero to 5 mm. Length-frequency distributions of the 1998 cohort differed significantly between October and March at sites 1 and 2 (Figure 17), and mean length increased 14 - 27 mm. No statistical comparisons were conducted for site 3 due to the low number of freshwater drum collected in March 1999.

McInerney and Held (1995) found growth in length of age-0 freshwater drum ceased between 9-11°C. In this study, water temperatures following October samples in both years remained at or above 9°C through November 6 - 8 (1997) and December 8 - 9 (1998). This result suggested differences in mean length of freshwater drum between October and March could be attributed to growth between sampling periods rather than size-selective overwinter mortality. To test this hypothesis, I regressed changes in mean length (mm) between October and March on the number of days between October and March samples where water temperatures were greater than or equal to 9°C. This *post-hoc* analysis indicated that 95% of the variation in length differences between October and March was attributed to water temperature greater than 9°C (Figure 18).

Catch per effort of age-1 freshwater drum sampled in March 1998 (mean = 1.04/min) and March 1999 (mean = 1.15/min) did not differ significantly between years ($F = 0.04$, $df = 1, 16$, $P = 0.85$) or among sites ($F = 2.12$, $df = 2, 16$, $P = 0.15$). Catch per effort values were generally highest at site 1, and averaged 1.97/min (site 1), 0.27/min (site 2), and 0.88/min (site 3) in March 1998. Mean C/f in March 1999 was 1.95/min

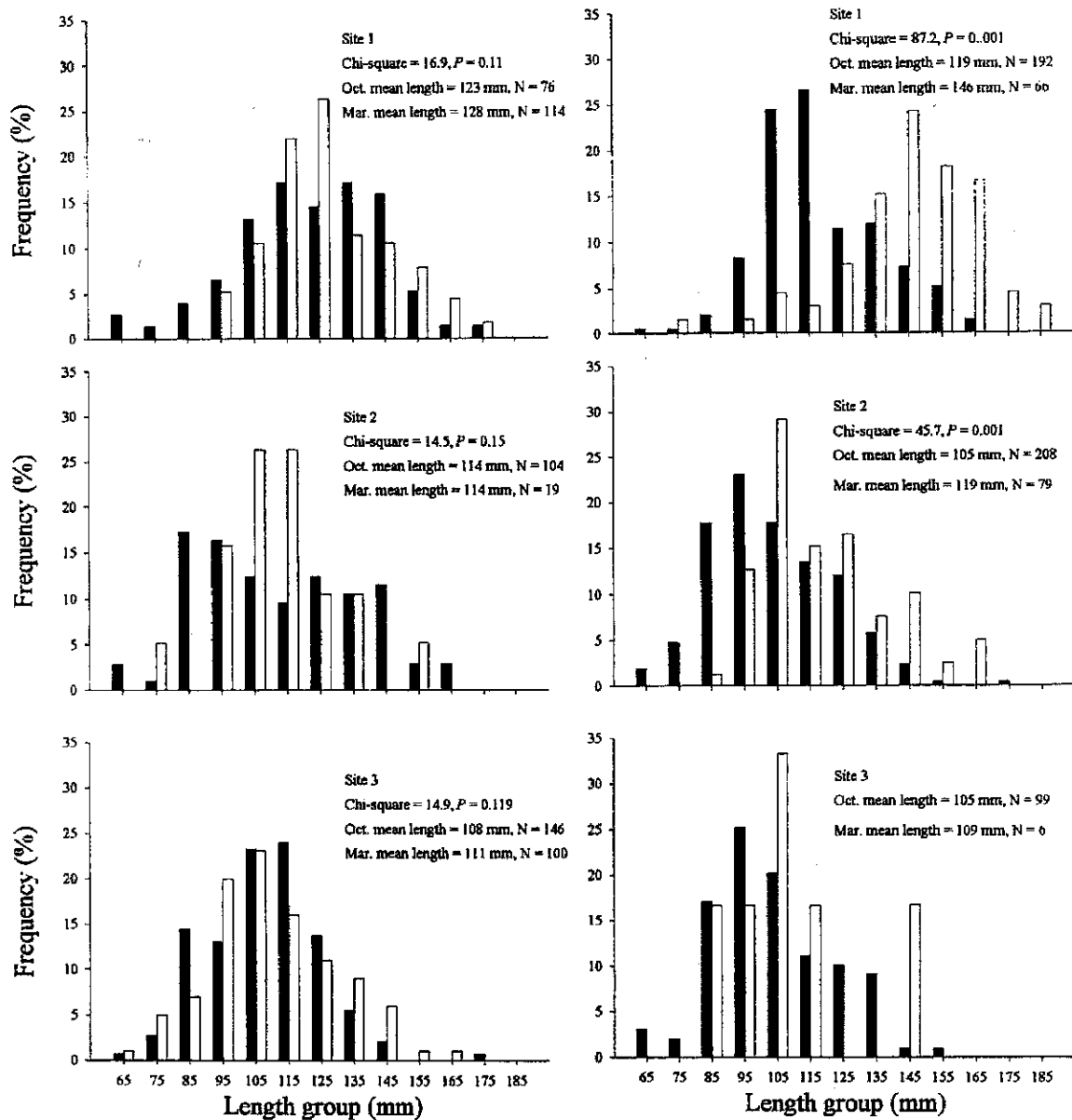


Figure 17.-Length-frequency histograms of age-0 (solid bars) and age-1 (open bars) freshwater drum collected at sites 1, 2, and 3 in the channelized Missouri River during October 1997 and March 1998 (left panel) and October 1998 and March 1999 (right panel).

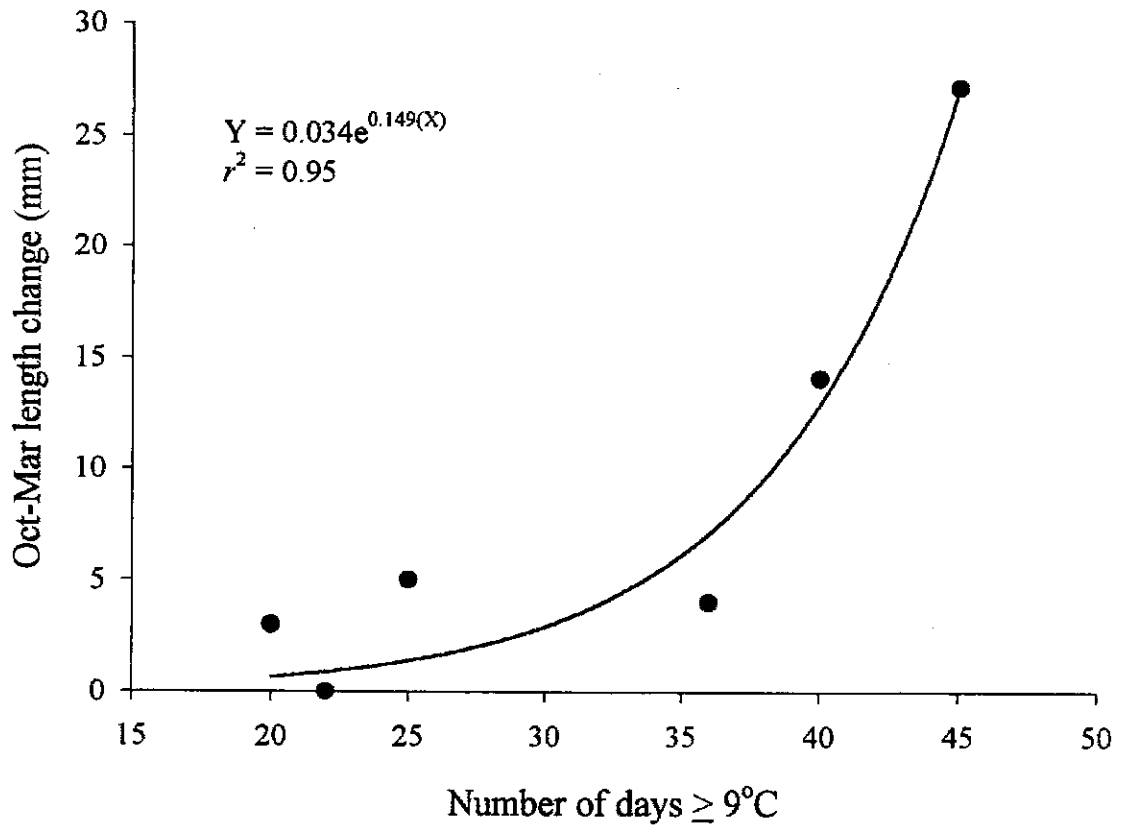


Figure 18.-Relationship between site-level change in mean length of freshwater drum between October (age-0) and March (age-1) and number of days where water temperature equaled or exceeded 9°C in the channelized Missouri River.

(site 1), 1.38/min (site 2), and 0.12/min (site 3). There was no relationship between C/f of age-0 individuals in October and age-1 individuals in March ($r^2 = 0.07$, $P = 0.59$; Figure 19); however, there was an unusually high C/f of age-1 individuals at site 1 during March 1998 which strongly influenced the relationship. Removing this data point significantly improved the model ($r^2 = 0.86$, $P = 0.022$; Figure 19).

Discussion

Larval Freshwater Drum

Despite the widespread recognition that eggs and larvae of numerous fish species in lotic ecosystems are prone to downstream transport (Cada and Hergenrader 1980; Holland and Sylvester 1983; Muth and Schmulbach 1984; Brown and Armstrong 1985; Sheaffer and Nickum 1986; Harvey 1987; Turner et al. 1994; Holland-Bartels et al. 1995; McInerney and Held 1995; Rider and Margraf 1997; Mitro and Parrish 1997; Jurajda 1998; Mion et al. 1998; Robinson et al. 1998), few studies have examined the importance of this process in regulating spatial patterns of fish distribution and abundance (Robinson et al. 1998). The spatial and temporal patterns of larval freshwater drum observed in this study were strongly linked to differences in larval sources between years. In 1997 when larval freshwater drum were small (median = 4.2 mm) and young (median age = 3 days), each source contributed about one-third of the larval production. These results indicated that continual spawning and larval additions occurred throughout the reach from Gavins Point Dam through the channelized river. This conclusion is also supported by the finding that larval densities and distance downstream from Gavins Point Dam were not

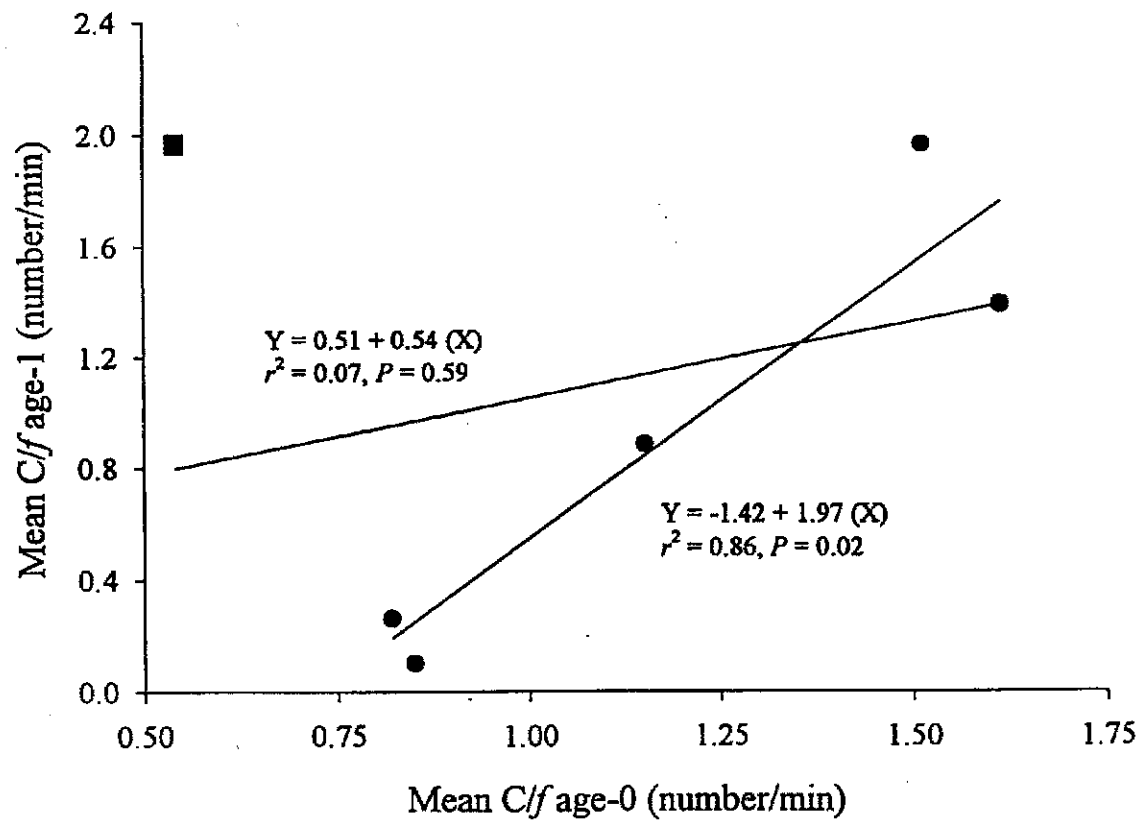


Figure 19.-Relationship between mean C/f of age-0 freshwater drum in October and age-1 freshwater drum sampled the following March in the channelized Missouri River. The nonsignificant ($P = 0.59$) regression line includes all data, and the significant ($P = 0.02$) regression line does not include the outlier (square symbol).

highly correlated, and that larval densities did not differ among sites. In contrast to 1997, larval freshwater drum sampled in 1998 were larger (median = 9 mm) and older (median age = 14 days) indicating that larvae were primarily derived from a single distant, upstream source. Additional support for this conclusion is provided by several lines of evidence. First, the strong correlation between larval densities and distance downstream from Gavins Point Dam indicated cumulative settlement of larger larvae reduced densities from upstream to downstream sites. Second, coupling larval ages with river travel time indicated Lewis and Clark Lake contributed greater than 78% of the larvae collected at all sites. Third, the peak density of larvae during July 1 indicated a pulse of larvae comprised of several age classes exited Lewis and Clark Lake, and remained in suspension until they reached a size suitable for settlement. After a 7-day period of reduced outflows from Gavins Point Dam, discharge was incrementally increased during June 23 - June 26. The increased discharge likely flushed larval freshwater drum from Lewis and Clark Lake to the Missouri River where they remained in suspension for the 5 - 8 day travel time to the study sites. This result is consistent with the instream transport and maturation hypothesis posed by Hergenrader et al. (1982) in the upper channelized Missouri River. Walburg (1971) estimated that a maximum of 10 million larval freshwater drum passed through Gavins Point Dam on a daily basis. He found that 50 - 80% of the freshwater drum passed through Gavins Point Dam over a relatively short time interval (e.g., 3-10 days) which is consistent with the temporal pulse of larvae observed in this study. Long-distance dispersal of larvae from spawning areas to settling areas is not limited exclusively to high-velocity rivers such as the channelized Missouri

River. Danilowicz (1997) found Hawaiian domino damselfish *Dascyllus albisella* drifted 12 - 36 days in oceanic current velocities of 10 km/day before arriving at settling areas 120 - 360 km down-current from spawning locations.

Higher density of larval freshwater drum and greater contributions from Lewis and Clark Lake in 1998 could be attributed to differences in reproductive success between years. Trawl catch rates of larval freshwater drum in Lewis and Clark Lake were 9.9 times greater in 1998 (mean = 119 larvae/min) than 1997 (mean = 12 larvae/min; Nebraska Game and Parks Commission 1997, 1998). Thus, higher densities and greater contributions from Lewis and Clark Lake in 1998 may reflect the higher abundance of larval freshwater drum in Lewis and Clark Lake. Conversely, the abundance of larval freshwater drum originating from the channelized and unchannelized reaches of the river was greater in 1997 than 1998. The difference in abundance between years reflects differential reproductive success in the lotic portions of the river between years which may be related to temporal dynamics in water temperature and discharge. For example, water temperature in the channelized and unchannelized river sections were more variable in 1998 than 1997. After spawning started in early June 1998, water temperature rapidly declined 6.3°C in the channelized reach, and 4.5°C in the unchannelized reach. Low or rapid declines in water temperature have been shown to cause mortality of eggs and larvae in other species (Dey 1981; Uphoff 1989). As a consequence, survival of freshwater drum eggs and larvae may have been less affected in Lewis and Clark Lake than in the unchannelized and channelized reaches in 1998. The lack of small freshwater drum in sampling periods following the rapid temperature declines further supports this

conclusion. Similar to water temperature, discharge in the unchannelized and channelized reaches was more variable in 1998 than 1997 which may have accounted for the disproportionate contribution from Lewis and Clark Lake in 1998. High flow events such as those which occurred in mid-June 1998 displace and kill larval fishes (Harvey 1987; Mion et al. 1998).

Determination of sources of larval freshwater drum was based on the assumptions that 1) tributaries in the reach between Lewis and Clark Lake and site 3 were not significant sources of larval freshwater drum, 2) larval freshwater drum act as passively drifting particles in the river current until they reach a size that facilitates active settlement from the current, and 3) entrainment in eddy pools created by wing-dikes did not confound river travel time estimates. For the first assumption, Hergenrader et al. (1982) determined seven Missouri River tributaries in the channelized river between Sioux City, Iowa and Leavenworth, Kansas (between sites 1 and 2; Figure 1) contributed 0.15% of the total larval freshwater drum collected from main channel and tributary habitats. Muth and Schmulbach (1984) found the James River (confluence located in the unchannelized Missouri River downstream from Gavins Point Dam; Figure 1) contributed freshwater drum to the Missouri River; however, mean density of freshwater drum was generally low ($0.1/\text{m}^3$) and peak density did not exceed $0.323/\text{m}^3$. Based on results from these studies, tributaries contribute larval freshwater drum to the Missouri River; however, the contribution is slight in comparison to the overall densities of larval freshwater drum in the Missouri River. Several studies provide support for the second assumption. For example, eggs and larvae of freshwater drum are buoyant (Swedberg

and Walburg 1970) which makes these early life stages susceptible to current transport. In Lewis and Clark Lake, freshwater drum spawn primarily in the middle and upper reaches of the reservoir (Swedberg and Walburg 1970); however, larvae and juveniles are entrained in the intake area of Gavins Point Dam at the lower end of the reservoir (Walburg 1971). Low water velocities in Lewis and Clark Lake (i.e., 0.10 to 0.47 m/s) are sufficient to transport larvae and juveniles from up-reservoir spawning areas to down-reservoir areas (Walburg 1971). In the channelized Missouri River, turbulence and water velocities are high (Harrow et al. 1975; Slizeski et al. 1982), and Hergenrader et al. (1982) determined that larval freshwater drum act as passively drifting particles in this high-velocity environment. Furthermore, the estimated length at larval settling (9.7 mm) is similar to the length (10 mm) at which freshwater drum in Lewis and Clark Lake move from pelagic to benthic habitats (Swedberg and Walburg 1970). Danilowicz (1997) similarly found Hawaiian domino damselfish settle at 10.2 mm, and Forrester (1995) found bridled goby *Coryphopterus glaucofraenum* settled at 10-13 mm. Harvey (1987) also found susceptibility of fishes to current displacement declined at lengths greater than 10 mm. Larval freshwater drum have been collected in eddy pools created by wing dikes (Hergenrader et al. 1982). These individuals are likely from the main-channel drift community, and become entrained into these habitats. To my knowledge, no studies have examined water residence time in wing-dike pools (time for an eddy pool to completely replaced with new river water) or studied how residence time would affect longitudinal transport in the Missouri River. High residence time could bias freshwater drum source estimations by over-estimating the location upstream where the individual was spawned.

For example, if an individual 4-days old was collected at site 2, that individual's estimated spawn location would be the unchannelized river. However, if the individual spent a cumulative period of one or more days entrained in one or more wing dike pools, the actual spawning location for the individual would be the channelized section of the Missouri River. Only a small fraction of the total water volume in the river enters a given wing dike at a particular point in time. Therefore, it is likely that the number of larvae entering the wing dike pool is also small in comparison to the total number of larvae drifting in other channel locations. I believe entrainment into wing dike pools has a minimal effect on the estimation of larval freshwater drum sources.

Instantaneous growth rates of larval freshwater drum in this study were similar to those in the Mississippi River (Zigler and Jennings 1993), but greater than those reported by Cada and Hergenrader (1980) in the channelized Missouri River in Nebraska. However, Cada and Hergenrader (1980) used a length-based method (e.g., Hackney and Webb 1978) to determine growth rates making direct comparisons of growth rate between studies difficult. Zigler and Jennings (1993) found instantaneous growth rates of larval freshwater drum determined from otoliths exceeded those from length-based methods in three of four cases. Swedberg and Walburg (1970) found larval freshwater drum grew at an average rate of 0.38 mm/day during the first four days post-hatch in the laboratory. Larvae from Cada and Hergenrader (1980) had an average growth rate of 0.14 mm/day during the first four days post-hatch. Freshwater drum growth in this study averaged 0.27 mm/day during the first four days post-hatch.

Growth of larval freshwater drum in the Missouri River may be influenced by larval density and sources. For example, growth rate was slightly greater in 1997 when larval densities were lower and several sources contributed to the freshwater drum population. In contrast, lower growth rates occurred during 1998 when the majority of larvae collected originated from a single source. Because larval growth and density are inversely related (Wang et al. 1997), lower growth rates of larval freshwater drum in the Missouri River may result when the majority of larvae are reared in a single source at high densities.

The two-stage pattern of decreasing mortality with increasing age observed in 1997 is typical of larval fish populations (Dey 1981; Crecco and Savoy 1987; Uphoff 1989; Houde 1997). Cada and Hergenrader (1980) calculated instantaneous mortality values ranging from 0.11 to 0.24 for larval freshwater drum 8 - 33 days old which are comparable to my estimates for larvae 7-14 days old. Zigler and Jennings (1993) in the Mississippi River estimated mortality rates varying between 0.20 and 0.43 for larval freshwater drum 6-12 days old.

Age-0 Freshwater Drum and Overwinter Survival

Much debate has centered on identifying factors regulating fish recruitment in demographically open populations (Caley et al. 1996). Although annual variations in the supply of larvae due to biotic and abiotic factors will ultimately influence initial larval numbers available for colonization and establishment of populations, the extent by which population density is regulated by density-independent, non-equilibrium processes (sensu Doherty and Williams 1988; Doherty 1991) and/or density-dependent factors remains

controversial. Lewis and Clark Lake was the single source of larval freshwater drum available for colonization of habitats in the lower channelized Missouri River. Although the channelized and unchannelized reaches were temporally important sources of larval production, all settling-sized individuals for each site were spawned in Lewis and Clark Lake. Catch per effort of age-0 freshwater drum in October correlated highly with settler density in both years; however, *C/f* of age-0 freshwater drum increased rapidly with increases in settler density when settler density was low (1997), but increased at a much slower rate when settler density was high (1998). As a consequence, settler density averaged 251 times greater in 1998 than 1997, but age-0 *C/f* was only 1.57 times greater in 1998. These results suggest that abundance of age-0 freshwater drum in the channelized Missouri River is strongly regulated by larval supply at low densities of settlers (e.g., recruitment limitation), but by other mechanisms when settler densities are high. Several authors have found that density - dependent factors influence the relationship between larval and juvenile densities (Forrester 1995; Caselle 1999; Schmitt and Holbrook 1999a, 1999b). Post-settlement mortality may have contributed to the suppressed abundance of age-0 freshwater drum in 1998. Schmitt and Holbrook (1999a) found populations of damselfish (*Dascyllus* sp.) settlers were reduced 47-53% during the first two weeks after settlement, and Victor (1986) found densities of bluehead wrasse *Thalasoma bifasciatum* were reduced about 20% during the first three days of settlement. Other factors including predation, food limitations, shelter, and emigration (Jones 1991; Forrester 1995; Levin 1998; Schmitt and Holbrook 1999b) may similarly have suppressed abundance of age-0 freshwater drum in 1998. Butler (1965) suggested the abundance of

young freshwater drum in the Mississippi River was not strongly regulated by predation; however, several piscivores including flathead catfish, sauger, and channel catfish (Hesse et al. 1982) occur in the Missouri River, and may feed on young freshwater drum. Wahl and Nielsen (1985) found freshwater drum composed 16% of the diet of sauger in the Ohio River. Competition for food and shelter are also likely sources of mortality of young freshwater drum after settlement.

Differential sampling of larval freshwater drum from inside bends and age-0 individuals on outside bends introduced a potential source of error in relationships between settler densities and age-0 C/f in October at all sites. For example, Hergenrader et al. (1982) in the channelized Missouri River found density of larval fish on outside bends averaged 1.58 times greater than density on inside bends, but was significantly correlated with density on inside bends ($r = 0.92$, $P = 0.0002$, $N = 10$). Underestimation of settler density would inflate the y-intercept of the age-0 C/f - settler density relationship. This conclusion is supported by the finding that estimates of age-0 C/f in October were 0.53 (1997) and 0.67 (1998) at zero densities of larval settlers.

Decline in relative abundance of age-0 freshwater drum on outside bends among months was consistent between years and sites despite inter-annual differences in larval densities and age-0 abundance. Previous studies have determined that fishes emigrate from main channel habitats to wing dike pools during fall, and use wing dike pools as their primary over-winter habitat in the Missouri River (Hesse and Newcomb 1982; Newcomb 1989). These results corroborate those findings. However, the timing (e.g., month) of emigration and mechanisms influencing emigration have not been thoroughly

evaluated. Results from this study suggest several factors may directly or indirectly induce emigration and explain declines in the relative abundance of age-0 freshwater drum and other species from October to December. Strong positive correlations between C/f and water temperature suggest emigration was temperature-related. Significant declines in both years of the study occurred as water temperature declined from 16-18°C (October) to 8-10°C (November), and 1-8°C (December). Because viscosity and water temperature are inversely related (Gordon et al. 1992), individuals may have emigrated from higher velocity outside bend habitats to lower velocity wing dike pools to offset increased energetic demands. Declining C/f of age-0 freshwater drum between October and December was also accompanied by decreases in length, weight, and condition suggesting a size-related pattern of emigration. Large individuals may become habitat-limited if their length exceeds the maximum length capable of being supported by interstitial areas in the riprap. The effect of this restriction would be magnified as water temperature decreased due to temperature effects on viscosity and swimming abilities.

There was a consistent spatial pattern of decreasing length, weight, and K_n of age-0 freshwater drum in October from upstream to downstream sites. Lack of a significant year x site interaction in the growth analysis indicated the longitudinal pattern of first-summer growth was consistent between years despite the finding that site-level densities of larval freshwater drum settlers, C/f of age-0 freshwater drum, river discharge, and water temperatures did not exhibit consistent longitudinal patterns between years. These results suggest that length, weight, and condition of age-0 freshwater drum are influenced by factors that consistently differ from upstream to downstream. Differences in food

production from upstream to downstream may account for differences in growth.

Dieterman et al. (1996) and Young et al. (1997) reported a trend of increasing turbidity on outside bend habitats from upstream to downstream sites that may negatively influence aquatic production and growth of age-0 freshwater drum. Rutherford et al. (1995) found that growth of freshwater drum was enhanced during low turbidity conditions because primary and secondary production were greater under low than high turbidity conditions.

Between year differences in mean length and K_n of age-0 freshwater drum in October occurred in conjunction with significant annual variations in larval settling densities, age-0 abundance, and river discharge. However, greater mean lengths of the 1997 cohort, but higher K_n of the 1998 cohort suggest differential growth responses of freshwater drum between years. These differences were likely related to complex interactions involving river discharge and fish densities. Because velocity increases with increasing discharge in the Missouri River (Slizeski et al. 1982), freshwater drum during the 1997 growing season were exposed to higher velocity conditions. High velocities may select for larger individuals, and inflate mean length due to selective mortality of smaller individuals (Torralva et al. 1997). A second explanation for greater length but reduced K_n of the 1997 cohort of freshwater drum is differential growth allocation between years. One mechanism used by fishes to offset greater energetic demands and increased frictional drag associated with high velocities is to modify body morphology by increasing length (Gordon et al. 1992). Age-0 freshwater drum in 1997 were more streamlined (i.e., longer) than in 1998, but weighed less for a given length (i.e., lower K_n). Several studies have documented phenotypic plasticity in fishes in response to gradients

of environmental conditions (Beacham et al. 1988; Beacham et al. 1989; Torralva et al. 1997; Holopainen et al. 1997). The labile nature of phenotypic plasticity (sensu Scheiner 1993) supports the hypothesis that body morphology of age-0 freshwater drum may respond fairly quickly (e.g., within a growing season) to changes in Missouri River discharge and velocity. For example, Holopainen et al. (1997) demonstrated changes in body morphology of crucian carp *Carassius carassius* could be environmentally induced with complete phenotypic change occurring in three months.

Significant correlations between growth metrics of age-0 freshwater drum in October and total C/f in 1997 but not in 1998 suggest density - dependent regulation of growth may vary with Missouri River discharge. Although C/f of age-0 freshwater drum was generally lower in 1997, low-velocity habitat was more restricted due to high discharge, and contributed to competition for food and feeding locations. Other studies have similarly reported density-dependent growth in fish (Forrester 1990; Michaletz 1997; Wang et al. 1997; Post et al. 1998; Schlosser 1998). Intra- and interspecific competition do not contradict the conclusion that abundance of age-0 freshwater drum in 1997 was primarily regulated by larval supply and density-independent factors. Competition is a valid tenant under the recruitment limitation hypothesis to the extent that it only influences differential fitness among individuals, but does not directly regulate population size (Victor 1986). Lack of significant correlations between growth metrics and C/f in 1998 suggest compensatory factors (e.g., post-settlement mortality, predation, emigration) reduced populations of age-0 freshwater drum during the growing season to levels capable of being supported by the habitat (i.e., carrying capacity). These results

suggest that under low discharge conditions such as those in 1998, C/f of age-0 freshwater drum averaging 1.32/min (maximum = 1.61/min) represents an upper threshold of abundance.

Spatial and temporal variation in the abundance of settling larvae and age-0 freshwater drum did not significantly influence the likelihood of overwinter mortality, despite evidence for density-dependent control of growth and condition (i.e., 1997). These results do not support the hypothesis by Schlosser (1998) that spatial and temporal variations in trophic interactions mediated by varying fish densities play a strong role in regulating first-summer growth and energy acquisition, and consequently overwinter survival of juvenile fishes. Similarly, results from this study do not support the hypothesis that size-selective overwinter mortality is a significant factor regulating freshwater drum populations in the lower channelized Missouri River. Despite support for this hypothesis from other studies (Oliver et al. 1979; Toney and Coble 1979; Shuter et al. 1980; Conover and Ross 1982; Henderson et al. 1988; Post and Evans 1989; Johnson and Evans 1990; Miranda and Hubbard 1994; Kirjasniemi and Valtonen 1997; Hurst and Conover 1998; Post et al. 1998; Schlosser 1998; Schultz et al. 1998), several factors may account for the lack of size-selective overwinter mortality in this study. Post and Evans (1989) postulated that the occurrence of overwinter mortality due to starvation would likely decrease from north to south because length of the growing season increases and winter duration decreases from northern to southern latitudes. In this study, the growing season persisted through early November (1997) and early December (1998); whereas, cold winter conditions (e.g., $< 4^{\circ}\text{C}$) were only 48 - 84 days in duration. The

long growing season facilitated a high accumulation of energy stores as evidenced by high K_n in October. Wahl et al. (1988) also concluded that extended growing seasons in large rivers enhanced growth of freshwater drum. In the Mississippi River, Bodensteiner and Lewis (1992) found age-0 freshwater drum near the end of winter (March) still retained sufficient energy reserves. Thus, overwinter mortality due to complete exhaustion of energy reserves during winter is not common in lotic populations of freshwater drum (Bodensteiner and Lewis 1992), at least in mid-latitude areas.

Lack of evidence for size-selective overwinter mortality does not imply that populations of freshwater drum in the lower channelized Missouri River are not subject to overwinter mortality. Rather, stressful conditions such as extremely cold temperatures which disrupt physiological processes (Bodensteiner and Lewis 1992; Johnson and Evans 1996) may contribute to mortality independent of fish size (Schultz et al. 1998). Although October and March C/f values were linearly correlated at most sites, declines in C/f between October and March indicated the freshwater drum population was reduced 14-85% at sites 2 and 3 during both winters. Bodensteiner and Lewis (1992) found 56% mortality of freshwater drum exposed to 1°C water temperatures for 0-45 days. Average over-winter mortality at sites 2 and 3 was 47% for 14-20 days of exposure to water temperatures less than 1°C which is comparable to mortality estimates from Bodensteiner and Lewis (1992). These results suggest populations of age-0 freshwater drum are significantly reduced during winter through mechanisms independent of fish size. Site 1 is an exception to this conclusion, and it is unclear why mean C/f was 3.6 (1997 cohort) and 1.3 times (1998 cohort) higher in March than October, and generally higher at site 1

than other sites. One explanation is that high velocities in this section of the Missouri River (Slizeski et al. 1982) limit the availability of low-velocity wing dikes. This would tend to obscure relations between October and March C/f because freshwater drum would concentrate in limited numbers of wing dikes and inflate March C/f, rather than distribute more evenly among several wing dikes.

Implications of Differential Larval Sources to Fish Recruitment in Rivers

The close link between reproductive processes of fish and flow-mediated dispersal (active or passive) has important applications for lotic ecosystems. First, identifying primary and secondary sources of fish reproduction in lotic ecosystems is critical in source-sink and metapopulation models (Pulliam 1988; Caley et al. 1996; Simberloff 1997; Schlosser 1998). Because sources exhibit substantial spatial and temporal variation in the magnitude of their larval contributions, receiving populations may similarly experience highly variable demographic rates (e.g., immigration). Second, damming transforms rivers into a series of alternating lentic and lotic systems each of which may vary temporally and spatially in their magnitude as reproductive sources. Because lotic and lentic environments often have dissimilar fish species composition, differential spawning success in either environment may cause spatial and temporal shifts in species composition along the river. For example, Fisher (1962) conducted a qualitative study of fishes in the lower Missouri River during 1945, ten years prior to the closing of Gavins Point Dam in 1955. He found that freshwater drum at sites close to sites 1 and 2 in this study comprised 0.2% - 0.3% of all fish collected. In Lewis and Clark Lake, Walburg (1976) found catch rates of freshwater drum in gill nets increased between 1956 and 1972

following closure of Gavins Point Dam. These studies suggest that the abundance of freshwater drum was relatively low in the Missouri River prior to construction of Gavins Point Dam. Presently, freshwater drum is one of the most abundant species in the lower Missouri River. This result suggests the increased abundance and spawning of freshwater drum in Lewis and Clark Lake in combination with larval dispersal and settling have contributed to the increased the abundance of freshwater drum in the channelized Missouri River. The extent to which reservoirs function as upstream sources for downstream areas is strongly influenced by design characteristics of the dam. Gavins Point Dam is a significant source of freshwater drum and other species because water is drawn from the reservoir surface to the bottom. Larval contributions from reservoirs with hypolimnetic intake structures may be minimal (Wolf et al. 1996) if larval fishes in the reservoir are primarily restricted to the epilimnion. Third, temporal variations in age-0 abundance observed at a specific river location cannot be inferred to reflect reproductive output at that location because larvae were likely produced at a distant upstream source under physical and biological conditions different than those where individuals were collected. Identification and modification of factors limiting reproductive success in upstream areas will enhance reproductive success, and result in a less patchy distribution of fishes in downstream areas.

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Research needs

1. Conduct controlled experiments on Missouri River fishes to determine whether variations in growth along the latitudinal gradient of the Missouri River are due to genetic differences among populations.
2. Quantify aquatic invertebrate communities throughout the Missouri River to discern longitudinal patterns in food availability.
3. Examine the role of overwinter mortality as a mechanism regulating recruitment of fishes throughout the Missouri River basin.
4. Conduct controlled experiments to determine the influence of water velocity on growth and morphological plasticity of Missouri River fishes.
5. Initiate long-term monitoring on the Missouri River. Information could be used to further examine fish life history characteristics (e.g., growth, mortality, longevity, maturation, etc.), test growth - discharge models developed in this study, and further evaluate growth responses to discharge.
6. Further examine the role of larval fish transport and colonization as mechanisms influencing spatial variations in juvenile and adult abundance.
7. Investigate broad-scale movement patterns of adult fishes in the Missouri River to identify primary spawning areas and seasonal habitats.